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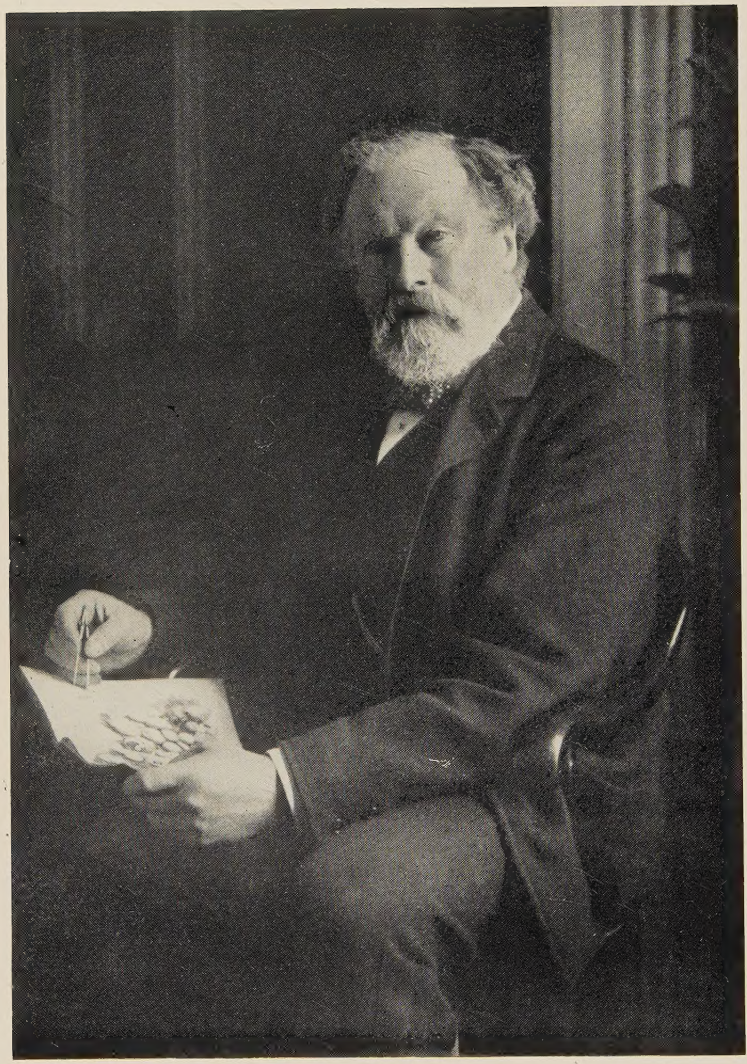

ARTHUR LISTER
(1830–1908)

THE LISTER MEMORIAL LECTURE

THE PHYSIOLOGY OF MYXOMYCETES

By LILIAN E. HAWKER

Department of Botany, University of Bristol

Not only in this country but throughout the world the study of the Myxomycetes or Mycetozoa is associated with the name of Lister. It is my very great privilege to have this opportunity to pay tribute to the brilliant but painstaking work of the Listers, father and daughter. All of us look to Arthur Lister's monograph on the Mycetozoa (1894, 1911, 1925) as the authority on taxonomy and nomenclature. Many of us remember the familiar figure of Miss Lister at our forays and remember also the results of her activities on these occasions, particularly her annual contribution to the specimen tables at the Epping Forays. It was with a real sense of loss that we learnt of Miss Lister's death in 1949 and we can offer no more fitting memorial to her and to her father than a revival of interest in the group they studied and loved. If my contribution to-day can point out to our younger members that here is a field which offers much of interest and of opportunity, then it will be a memorial lecture in the truest sense.

The early workers were concerned mainly with the life histories and systematic position of the Myxomycetes and Miss Lister (1913), in a presidential address to this Society, gave a fascinating account of the early work associated with such famous names as Linnaeus, Persoon, Elias Fries, Berkeley and de Bary. With the work of de Bary begins an interest not only in the taxonomy but in the physiology of these organisms, a subject which was further explored by Arthur Lister and which has recently received considerable attention.

Lister's monograph is confined to a consideration of the Exosporeae, which contains the single genus *Ceratiomyxa* in which the spores are borne singly, and the Endosporeae which includes a large number of genera in which the spores are borne within a sporangium. As is well known, the spores of these forms germinate under suitable conditions to give a characteristic swarm cell or zoospore which is usually, if not always, biflagellate although often appearing uniflagellate because of the small size of one flagellum (Elliott, 1949). From these cells develops the well-known reticulate plasmodium which may continue as a vegetative body for an indefinite period or may, under unfavourable conditions, pass into a resting stage or sclerotium or, under other circumstances, may produce the typical sporangia. The account of this life history given in Lister's monograph is still a model of descriptive writing. The saprophytic group of the Acrasiales, the members of which do not produce a true plasmodium until immediately before spore formation, the related group of the Labyrinthulales and the parasitic family of the Plasmodiophorales are sometimes included in the Myxomycetes, although recent work suggests

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that the relationship is not a close one (Martin, 1940). I am not here concerned with taxonomy, but since the physiology of the Acrasiales has been the subject of several careful studies and shows similarities to that of the true Myxomycetes, I shall include some references to that group.

Physiological studies, as might be expected, have been chiefly concerned with the factors influencing spore germination, with the nutrition of the plasmodium, with factors inducing sporulation and with the tactic movements of plasmodium and swarm cells in response to changes in the environment. In addition, the plasmodium has been a favourite object for the study of the composition and structure of protoplasm, but this work falls more appropriately into the fields of biochemistry and biophysics. The group has also received some attention as a possible source of antibiotics (Sobels, 1950).

Factors influencing spore germination

As with the spores of the true fungi so also with those of the Myxomycetes, germination depends upon both internal and external factors. Lister (1894) recorded that the length of time required for germination after the spores had been sown in water varied with the species and even in different collections of the same species. Typical dark spores of *Stemonitis fusca* germinated after 9–12 hr., while those of a pale-spored variety required only 28 min. Spores from freshly gathered material of *Reticularia lycoperdon* usually germinated in less than an hour but those from a specimen stored for 3 years required 4–20 hr. More recently Gilbert (1938, 1929) showed that the age of the spores and the degree of maturation were important. Spores of some species were unable to germinate immediately after formation and, in general, old spores germinated less readily than younger ones or were even unable to germinate. Gilbert considered that the conditions obtaining during sporangium formation influenced the degree of maturation, and consequently the ability of the spores to germinate. This may account for the failure of some experimenters to define conditions generally favourable to germination.

The effect of the physical factors of the environment has also received attention.

Lister (1901) induced germination of spores of *Badhamia utriculosa* by alternate wetting and drying, and this method was also found by Jahn (1907) and by Gilbert (1929) to increase the percentage germination of some species. Gilbert suggested that alternate freezing and thawing might be helpful.

In general, germination takes place over fairly wide ranges of temperature and of hydrogen-ion concentration. The species examined by Gilbert (1929) germinated at temperatures between 2 and 36° C., but the best results were obtained at 22–30° C. and particularly just below 30° C. Jahn (1907) was unable to induce germination of spores of a species of *Stemonitis* at 37° C., but exposure to that temperature for 5 min. did not prevent germination of spores after cooling. Most of the species examined by Gilbert (1929) germinated over a range of pH 4·0–8·0 and some could germinate over an even greater range. The optimum varied with the species from pH 4·5 to 7·0. Little is known of the effect of light on germination, and the results available suggest that spores of some species germinate more readily in light while those of others are favoured by darkness, but that the effect of light is not necessarily correlated with the conditions of lighting in the normal habitat (Cook & Holt, 1928).

Experiments on the effect of nutrient solutions on germination are at first sight contradictory since some observers (de Bary, 1864, 1884; Lister, 1894; McClatchie, 1894; Smith, 1929) obtained satisfactory germination in distilled or tap water while others reported improved germination in weak solutions of sugars, peptones or other pure substances (Constantineaunu, 1906; Cook & Holt, 1928) or in decoctions of such natural substrata as rotten wood, bark, hay, seeds, or soil rich in humus (Ward, 1886; Constantineaunu, 1906; Smart, 1937, 1938). As might be expected, different species varied in their requirements.

Most of these observers, however, took no particular precautions to prevent the inclusion of bacteria in their spore suspensions and it is obvious that, particularly with species slow to germinate, these contaminations would have a profound effect. Pinoy (1907) demonstrated that spores of *Dictyostelium mucoroides* plated out on gelatine developed only in the neighbourhood of bacterial colonies. The spores were freed from bacteria by treatment with chloroform, ether or heat but would not then germinate unless the appropriate bacteria were added. Wilson and Cadman (1928), working with the very rapidly germinating spores of *Reticularia lycoperdon*, found that single spores would not germinate in water but that if sown in large masses the spores germinated readily, while Smart (1938) showed that isolated spores could be made to germinate by sowing them in filtered liquid in which large numbers of spores had previously germinated. It is thus likely that germination is dependent upon a suitable concentration of some growth hormone which would be reached in dense suspensions of spores but not with small numbers, and which is readily produced by certain bacteria. Spores which are slow to germinate would almost certainly be heavily contaminated with bacteria before germination takes place, and the beneficial effect of sugars and proteins claimed for some species might well be due to the encouragement of bacterial growth rather than to a direct nutritional effect on the Myxomycete spores themselves.

There is obviously need for further work on the physiology of spore germination, but it is interesting to note that so far as our scanty knowledge extends we find considerable similarity in the factors favouring germination of the spores of the Myxomycetes and of those of the true fungi.

It is generally accepted that the swarm cells fuse in pairs before the formation of a plasmodium. Abe (1934) claimed that there was a sex difference between the fusing swarmers, since one tended to flow into the other, and that this difference was correlated with differences in staining reaction, oxidation-reduction potential and electrical charge, but this could not be confirmed by Kambly (1939). The suggestion, however, is of sufficient interest to justify further investigation.

Nutrition and development of swarm cells and plasmodia

Investigators too numerous to list have attempted to cultivate various species of Myxomycetes. Earlier workers merely brought into the laboratory pieces of rotten wood, moss or dead leaves, bearing plasmodia or sporangia of a Myxomycete and allowed the latter to develop in a moist atmosphere. Many of these observers were concerned mainly with the study of life history, and their remarks on nutrition and cultivation were merely incidental. Nevertheless, such work produced much information on the ability of various species to consume fruit-bodies and mycelia of various fungi (Lister, 1888; Elliott, 1916; Howard, 1931; Howard & Currie, 1931, 1932).

While it was soon recognized that the plasmodium was able to digest solid particles in the vacuoles, it was not until 1889 that Lister conclusively proved that the swarm cells could also surround and digest solid food such as bacterial cells, but that while inorganic particles might be engulfed they were later discharged. Gilbert (1928) showed that the ability of swarm cells of *Dictydiaethalium plumbeum* to digest fungal spores depended upon these being of suitable size. Large spores were attractive to the swarmers but could not be ingested. Others germinated rapidly to produce hyphae which were also too large. Others such as *Trichoderma* were ingested but discharged, some were digested except for oil globules and yet others, including spores of *Penicillium* and *Aspergillus*, were repellent to the swarmers and were merely engulfed but still not digested when killed by heat or treated with alcohol.

Many of these earlier workers ignored the presence of contaminating bacteria and other organisms in their cultures, and it is obvious that more exact methods are essential in work on nutrition. Numerous attempts have been made to establish various species of Myxomycetes in pure culture but few of these have been successful. It is still undecided whether these organisms can be maintained for any length of time in pure culture. A number of species, however, have been cultivated in what Pinoy (1907) quaintly refers to as 'pure-mixed cultures' and Cohen (1939) more accurately terms 'two-member cultures', that is, in the presence of only one other organism. In a few recent experiments I have found great difficulty both in freeing plasmodia from bacteria and moulds and in maintaining pure cultures obtained from other workers through more than one or two sub-culturings.

The role of bacteria in the nutrition of members of the Acrasiales has received detailed attention. Nadson (1899) claimed to have isolated *Dictyostelium mucoroides*, but his pure cultures developed irregularly and soon died. Cultures of this organism in association with *Pseudomonas fluorescens* var. *liquefaciens* grew well and Nadson concluded that the relationship was symbiotic. This has been disproved by later workers and it is now known that the Myxomycete actually consumes the bacteria. Vuillemin (1903) claimed that, while the organism could develop in the absence of bacteria, these when present were readily ingested in the vacuoles. In contrast, Potts (1902) maintained that *Dictyostelium* could not live in the absence of bacteria but that these were attacked by an extracellular enzyme. Pinoy (1907) agreed that the bacteria were surrounded and digested in the vacuoles. He concluded that *D. mucoroides* is unable to develop without at least the initial presence of bacteria and obtained similar results with *D. purpureum* and *Polysphondylium violaceum*. The relationship between bacteria and *Dictyostelium discoideum* has been studied in detail by Raper (1939). He used an agar medium containing peptone and a carbohydrate, and demonstrated that *Dictyostelium* was able to grow only when conditions were such that the particular bacterium with which it was growing did not render the medium unduly alkaline. The presence of a fermentable carbohydrate helped to maintain this favourable acidity, since the acids formed by the bacteria during fermentation neutralized the ammonia produced from the peptone. Similarly, the buffering of the medium or the addition of drops of acid to the plate during development of the organisms, or the presence of an acid-producing fungus, favoured the development of *Dictyostelium*. Thus the initial composition of the medium acted indirectly on the Myxomycete which obtained its nourishment by direct consumption of the bacteria.

Klebs (1900) was the first investigator to cultivate the plasmodia of true Myxomycetes (species of *Didymium*) on a nutritive agar. He used an infusion of bean leaves as a source of nutrient but took no particular care to exclude bacteria so that his work does not give information as to the source of nutrient used by the slime mould. Henneberg (1901) and Chrzaszcz (1902) showed that both myxamoebae and plasmodia could ingest and kill living yeast cells, but Chrzaszcz offered the curious interpretation that the two organisms were in competition for food and that the Myxomycete destroyed the yeast cells but either voided them or used them merely as a subsidiary source of nourishment.

Pinoy (1907) established two-membered cultures of *D. difforme* and *D. effusum* with appropriate bacteria. He sowed spores of the Myxomycetes on agar slants and found that these only developed in tubes in which bacterial colonies also developed. Vouk (1913), Skupienski (1928) and von Stosch (1935) also grew species of *Didymium* in two-membered cultures with various bacteria, yeasts and moulds, but attempts to grow pure cultures on killed bacteria were unsuccessful. Watanabe (1932, 1933) cultivated a number of species with various bacteria and yeasts on plain washed agar, and so demonstrated that the plasmodia were able to derive their nourishment solely from other micro-organisms. Cohen (1941) could obtain no evidence of specificity of the bacteria associated with a particular species of Myxomycete, but bacteria were unsuitable if they changed the hydrogen-ion concentration of the medium too rapidly or if they grew poorly on the particular media employed.

While, by a suitable technique, it is thus possible to grow Myxomycetes in culture with only one other kind of organism, it is much more difficult to obtain them in pure culture. Skupienski (1927) claimed to have grown *D. nigripes* in pure culture but he took the clarity of the agar on which the plasmodia were growing as proof of the purity of his cultures. Similarly, Howard (1931 *a*) claimed to have purified cultures of *Physarum polycephalum* by repeated transfer on plain agar. He pointed out that media suitable for the growth of plasmodia should not only allow vigorous growth, but should provide support to allow easy transfer and should consist of inexpensive ingredients available throughout the year. These conditions were fulfilled by oatmeal agar. It is obvious that inspection of such a medium would not necessarily reveal the purity or otherwise of a culture. Camp (1937) grew the same species on moist paper or gauze on which dry rolled oats were sprinkled twice daily. Both these methods are excellent for producing a large supply of plasmodia for experimental purposes, but it is doubtful whether either would readily yield a pure culture. Both methods have been critized by Cohen (1939), who himself succeeded in producing genuine pure cultures of a number of species. He suggests that satisfactory criteria of the purity of Myxomycete cultures are: (1) there must be no growth of other micro-organisms in a range of nutrient media inoculated from the alleged pure cultures; and (2) the cultures must be maintained through several transfers without loss of vigour. He applied these criteria successfully to cultures isolated by the migration method, in which he allowed the plasmodia to crawl over several plates of plain agar in succession, and by the enrichment method. In the latter he grew the plasmodia on streaks of suspensions of washed living yeast cells on plain agar. This gave a vigorous plasmodium which was then allowed to migrate over plain agar to rid itself of living yeast cells. The pure cultures, in contrast to two-membered cultures, did not grow well on oatmeal agar but grew on an agar medium with washed, autoclaved yeast as sole source of food. Preliminary experiments showed that the plasmodia could sometimes become adapted to originally unfavourable conditions.

Bonner (1947) claimed to have freed *Dictyostelium discoideum* of contaminating organisms by centrifugation, but this method, while suitable for the Acrasiales, is applicable to the spores and not to the plasmodia of the true Myxomycetes.

Recently Sobels (1950) has studied the nutrition of *Licea flexuosa*. This grew well on malt or oat gelatine in the presence of living cells of the yeasts *Torulopsis laurentii* or *Saccharomyces cerevisiae* or in pure culture with an autoclaved suspension of cells of the former but not the latter organism. Moreover, the Myxomycete grew on gelatine with peptone or asparagine. Growth on the latter medium was as good as with yeast extract and was further increased by the addition of sugars (of which trehalose was the best) but was not improved by the further addition of an alcoholic extract of yeast. Ammonium salts could not replace asparagine. Sobels extended the investigation to a number of other species and concluded that the true Myxomycetes fall into two nutritional groups: first, parasitic or saprophytic forms which retain the yellow-orange pigmentation of the plasmodia under any conditions and which are easily purified and grown in pure culture; and secondly, parasitic forms which are difficult to cultivate and which readily lose their pigment but regain it in mixed culture with other suitable organisms.

Thus while the elaboration of pure culture methods represents a great step forward, the exact study of the actual food requirements of the Myxomycetes has hardly been started. Such studies as that of Sobels could be elaborated and would certainly yield results of great interest.

THE EFFECT OF EXTERNAL CONDITIONS ON THE TYPE OF GROWTH

Very little exact work has been done on the effect of other environmental conditions on the development of the plasmodium. It is generally assumed that the maintenance of the active vegetative condition depends on adequate moisture, a suitable temperature and, as shown above, a favourable hydrogen-ion concentration. Changes in these conditions may lead to dormancy or spore production. Thus most observers are agreed that very dry conditions lead to the development of the sclerotial stage in which condition the organisms can be conveniently stored in a dry place for considerable periods. Subsequent moistening of the 'sclerotia' then induces the resumption of the plasmodial phase. There is less agreement as to the conditions which induce the formation of sporangia.

Partial desiccation, the nature and acidity of the substrate, light and injury have been postulated as causing the initiation of sporangial formation, but in the earlier literature these suggestions have been based on field observations and not on exact experiments.

Klebs (1900) maintained plasmodia of *Didymium difforme* and *D. squamulosum* in an active condition for an indefinite period by frequent transfer to fresh nutrient material, but if a portion were transferred to a moist nutrient-free substrate, sporangia were soon produced. Camp (1937) grew plasmodia of *Physarum polycephalum* on moist filter-paper with rolled oats as source of food and demonstrated that, if other conditions were favourable, the plasmodium continued to feed and grow as long as food was available but if the oats were not replaced sporulation took place. He showed that the interval between the last feeding and the onset of spore production increased with increase in the number of feedings, thus indicating that a well-nourished plasmodium is less likely to produce spores than one which has had only just sufficient food. Howard (1931) obtained sporangia of *P. polycephalum* most readily when the plasmodium was feeding on fungal cultures but other observers have not considered the effect of the nature of the food material available. This is obviously a promising field for investigation now that the technique of pure culture has been worked out.

Hydrogen-ion concentration influences the production of sporangia. Thus Emoto (1932) claimed that of some hundred collections nearly all the fruiting specimens were from acid substrata, and Raper (1939) showed that *Dictyostelium discoideum* produced spores only in a suitably acid medium. Gray (1939) concluded that while *Physarum polycephalum* fruited best in a rather acid medium (pH 3·0) the effect of acidity was interdependent with that of temperature and that the optimal acidity increased with rise in temperature up to a maximum of 32·5° C. If the hydrogen-ion concentration were constant the time for sporangial production varied with the temperature. In another paper the same investigator (Gray, 1938) showed that those forms with a yellow plasmodium needed light for spore production while the non-pigmented forms, as previously shown by Vouk (1910), would fruit either in light or darkness. In spite of the general belief that sporangia form in slightly drier conditions than those favouring vegetative growth there have been no exact experiments on this subject, and it is certain that conditions were moist in many of the experiments described above, while Cayley (1929) states that in her experiments, which were admittedly non-exact, sporangial formation did not necessarily depend on drier conditions. Many observers report, however, that the plasmodia migrated from the moist substrate on to the wall of the culture vessel before fruiting. The effect of aeration seems to have been neglected.

Thus such exact knowledge as we possess on this subject indicates that the conditions inducing spore formation in the Myxomycetes are in general similar to those causing sporulation in the true fungi. Seifriz and Russell (1936), however, maintain that fruiting of Myxomycetes is entirely dependent on an inherent rhythm which cannot be broken by such external factors as dryness, depletion of nutrition, character of substrate, temperature, light, poisons, pH, radium radiation or other injury. These authors admit, however, that nutrition and toxic action may have some effect, while Gray (1938), although recording that fruiting takes place at regular intervals, shows that this rhythm can be altered by changes in environmental conditions.

TACTIC MOVEMENTS OF SWARM CELLS AND PLASMODIA IN RESPONSE TO EXTERNAL STIMULI

From early times until the present day considerable interest has been aroused by the creeping movements of Myxomycete plasmodia. Frequent attempts have been made to determine the external stimuli which cause these movements and those of the swarm cells, but the mechanism is still not understood.

Hofmeister (1867) was the first to report movement of Myxomycete plasmodia in response to light and claimed that they were positively phototactic. Rosanoff (1868), however, considered that gravity was the controlling factor, while Baranetzki (1876) thought that light was the more important stimulus and that it could counteract the effect of gravity. The matter was further complicated by the opinion of Jönsson (1883) who maintained that Rosanoff had actually been dealing with negative rheotaxis.

Stahl (1884) suggested that light, gravity and flowing water were all important stimuli, but that water content and chemical nature of the substrate and temperature gradients all played a part in controlling the movements of the plasmodium. He suggested that thermotaxis might be of importance in determining the movements of the plasmodium before and after its seasonal perennation.

Later work was based on more exact technique. Wortmann (1885) showed that positive thermotaxis gave place to a negative movement above a critical temperature. This was confirmed by Clifford (1897) for *Fuligo varians* for which the critical temperature was 33–34° C. He also showed that this organism moved against a weak current of water, moved with a stronger one and moved out of the water if the current were excessively strong. Keferstein (1927) considered that hydrotaxis was of greater importance than rheotaxis, with which it is easily confused. Neither this worker nor Vouk (1910) could demonstrate any response of the plasmodium to gravity.

Stange (1890) claimed that various chemicals exerted positive or negative effects on swarm cells. More recently, Bonner (1947) showed that the aggregation of the pseudo-plasmodia of *Dictyostelium discoideum* to form a plasmodium was controlled by a substance which he termed 'acrasin' produced by the organism itself. Emoto (1932) demonstrated a positive response of the plasmodia of various true Myxomycetes to weak acids, dilute sugar solutions, peptone, meat extract and portions of fleshy Basidiomycete fruit-bodies, and a negative one to strong acids or alkalis. The plasmodia were indifferent to some other substances including starch and asparagine.

Watanabe, Kodati and Kinoshita (1938, 1938*a*, 1939) and Kinoshita (1938, 1939) attempted to explain plasmodial movement as a result of a difference in electrical charge in the front and rear portions of the moving plasmodium. They claimed that this difference was increased by some substances such as heteroauxin and reduced by others, including those known to inhibit or reduce respiration. This hypothesis, while it is an attractive suggestion, is inadequate to explain the observed facts and it is clear that the whole subject of the nature and mechanism of tactic movements of plasmodia and swarm cells requires investigation by modern methods.

In conclusion it is clear that, although much is known already of the physiology of this interesting but relatively neglected group, much more remains to be discovered. The recent advances in the technique of two-membered and pure cultures are both an opportunity and a challenge to investigators who can combine the patience and brilliant powers of observation of the early naturalists, among whom Arthur and Gulielma Lister were outstanding, with that mastery of modern techniques which is essential in solving the many problems which I have indicated. The recent discovery that some of these organisms possess antibiotic activity against bacteria may stimulate interest in this group, but the primary objective must still be the elucidation of the mechanisms of the living organism.

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THE LISTER NOTEBOOKS

For sixty years Arthur Lister and his daughter, Gulielma Lister, recorded their observations on the 'Mycetozoa' in a series of notebooks which on the death of Miss Lister in 1949 were bequeathed to the Society. In addition to providing a fascinating day-to-day 'laboratory record' of the chief interest of two distinguished naturalists, the notebooks contain material on which the successive editions of the *Monograph* and many of the Listers' papers were based and it is felt that the existence of these seventy-four volumes should be placed on public record.

The Listers' method of notekeeping was simple. Strongly bound quarto (9 by 7 in.) exercise books of lined paper were used and notes were entered chronologically. As each book was finished it was indexed, and a general index to the series and a letter register were maintained in a large folio ledger. The record comprises accounts of the authors' own collections and experiments, notes on specimens submitted by collectors in all parts of the world for identification or for a critical opinion, and hundreds of water-colour drawings, all of high quality and many of considerable artistic merit. In addition, the gist of letters received was entered (if the originals were not inserted) and the draft replies frequently given. Photographs of correspondents and their homes are interspersed with illustrations of Myxomycetes and loosely inserted reprints of numerous papers. Of particular interest to members of the Society is the series of annotated annual meeting notices and details of noteworthy items for the lists of Myxomycetes which Miss Lister contributed to the foray records for so many years. These are often accompanied by foray photographs, and the 'foray postcards', sent to Miss Lister when age prevented her attendance at the meetings, are carefully preserved.

The main series is supplemented by similar books recording the results of the examination of specimens in the national herbaria and other notable collections and by books devoted to the material from a number of important collectors.

The notebooks may be roughly classified as follows:

Main series

Notebooks 1–49 (50 in all as no. 3 is in two parts).

The first entry was made by Arthur Lister in January 1887 (then in his fifty-seventh year); the last by Miss Lister on 19 August 1947.

Historical collections

British Museum (Natural History). Specimens 1–4179. 4 books.

'List of mounted specimens of Mycetozoa in the British Museum collection. Arthur Lister. July 1st. 1895. (A corresponding number is marked on the slide with a diamond.)' Specimens 1–881. 1 book.

Kew Herbarium Collection of Mycetozoa. Specimens 1–1774 and index. 4 books.

De Bary's Collection of Mycetozoa at Strasbourg University. 404 specimens. 1 book (April 1893).

Paris Museum Collection. 293 specimens. 1 book (December 1893).

Index to Kew, British Museum, Strasbourg, and Massee collections. 1 book.

Material from individual collectors

I. B. Balfour, 1 book; A. Blytt (Christiania), in Kew Collection book 3; Mrs John Drake, 1 book ('Indian Mycetozoa'); Robert E. Fries (Uppsala), in Rex book 2; H. J. Howard (Norwich), in Sturgess book 3; G. Massee, in Index to Kew, British Museum, etc.; E. Nyman (Uppsala), in Rex book 2; T. Petch (Peradeniya, Ceylon), 1 book; G. A. Rex (Philadelphia), 2 books; William C. Sturgess (U.S.A.), 3 books (1898–1936).

Miscellaneous

A folio ledger containing a general index and letter register; 4 books of miscellaneous indexes, etc.

The Listers corresponded at one time or another with most of the well-known (and many of the less-known) British mycologists and in addition with, among others: G. R. Bisby, M. Brandza, Y. Emoto, W. G. Farlow, F. A. Gilbert, H. C. Gilbert, R. Hagelstein, H. Hattori, F. von Höhnel, O. Jaap, E. Jahn, J. Jarocki, G. Klebs, Solms Laubach, T. H. Macbride, G. W. Martin, M. Mijoshi, K. Minakata, C. Meylan, O. Penzig, H. Schinz, C. L. Shear and F. X. Skupienski.

Most important specimens were deposited by the Listers in the British Museum collection of Myxomycetes in which they took a life-long interest. Miss Lister's own herbarium and books from her library were bequeathed to Mr H. J. Howard of Norwich who has presented a number of reprints of the Listers' papers on Myxomycetes to the Society. A bibliography of the Listers' publications, prepared by Mr Howard, is being deposited with the notebooks.

Obituary notices

Arthur Lister (1830–1908). *Proc. Roy. Soc.* B, **88** (Obit. Notices), i–xi, 1915. (By J. J. L[ister].)

Gulielma Lister (1860–1949). *Trans. Brit. mycol. Soc.* **33**, 165–166, portr., 1950. (By E. M. W[akefield].) *Nature, Lond.*, **154**, 94, 1949. (By J. Ramsbottom.)

G. C. Ainsworth

A FURTHER NOTE ON SIZE AND FORM IN AGARICS

By T. E. T. BOND
Bracken Hill, University of Bristol

(With 3 Text-figures)

Measurements of 1166 illustrations from Lange's *Flora Agaricina Danica* confirm that there is a tendency for small agarics to be relatively tall with thin stalks, and for large agarics to be relatively short with thick stalks, as compared with the 'average type'. Thus, the cube of the pileus diameter tends to vary in proportion to the square of the stipe width, and the pileus diameter itself is proportional to the height of the sporophore above a limiting height of about 20 mm.

Ingold (1946) first concluded that the size and form of agaric sporophore are mutually determined by simple mechanical and functional principles involving proportional relationships between the volume of the pileus and the cross-sectional area of the stipe, and between the diameter of the pileus and the height of the sporophore above a certain limiting value (about 1·6 in.) regarded as the average minimum height for efficient spore dispersal. These relationships were deduced from the dimensions of some 500 species, given in Ramsbottom, *A Handbook of the Larger British Fungi* (1923) and derived in turn from an earlier publication by Smith (1908). A larger body of data, perhaps more objective in nature, is afforded by the illustrations to Lange, *Flora Agaricina Danica* (1935–40). A study of these illustrations confirms and extends Ingold's observations.

Apart from obviously unsuitable examples such as those of the excentric genera *Pleurotus*, *Panus* and *Crepidotus*, certain of the more deliquescent *Coprinus* species, and a few others, all drawings judged to be of fruit-bodies at full maturity were measured noting pileus diameter, total height of sporophore, and diameter of the stem near the middle. The measurements were made to the nearest millimetre. In all, 1166 individuals were recorded, representing more than 950 species.

Cap diameter and width of stipe

The average cap diameter for the 1166 determinations is 40·8 mm. (1·61 in.) and the average stipe width 6·8 mm. (0·27 in.). These are little more than half the corresponding averages for the species in Ramsbottom's *Handbook*, from which many of the smaller forms are omitted. According to Ingold's hypothesis, the weight of the pileus will depend on the mechanical strength of its support; i.e. the *cube* of the pileus diameter will be proportional to the *square* of the stipe width. This proposition has been tested graphically as shown in Fig. 1. For purposes of tabulation, the pileus measurements were first grouped at 5 mm. intervals. Then, the average pileus diameters (y) were obtained for successive arrays of stipe width (x) in millimetres, and their positions plotted. The theoretical $y^3 \propto x^2$ relationship was plotted from the corresponding logarithmic expression $3 \log y = 2 \log x + c$, as in the inset to the figure; c being determined by the values of the mean logarithms of x and y. The curve plotted, in other words, is that one joining the origin and the point representing the *geometric* mean values of $y = 68{\cdot}5$ mm. and $x = 12{\cdot}4$ mm. Ingold (1946, p. 109) based his discussion on a curve passing through the *arithmetic* mean values. I have found, on re-plotting Ingold's data, that the curve passing through the geometric means gives at least as close a fit. Fig. 1 shows clearly that the relation between size and form in the agaric sporophore, as illustrated by Lange, is far more adequately expressed by the logarithmic ($y^3 \propto x^2$) expression than by the linear ($y \propto x$). Differences

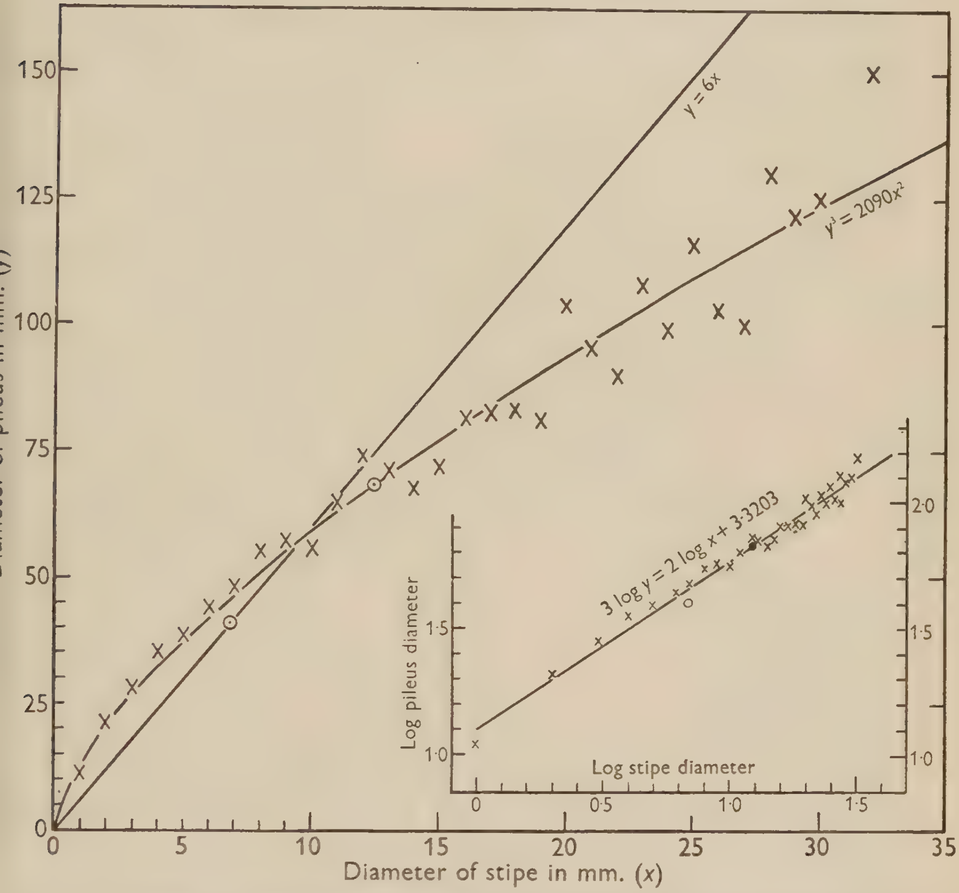

Fig. 1. Diameters of pileus averaged against diameters of stipe; 1166 determinations. The circles indicate the geometric ($y = 68{\cdot}5$, $x = 12{\cdot}4$) and arithmetic ($y = 40{\cdot}8$, $x = 6{\cdot}8$) mean values. *Inset*—the same, by logarithms, showing the derivation of the $y^3 \propto x^2$ relationship from the linear expression $3 \log y = 2 \log x + 3{\cdot}3203$. Circles indicate the means, as before.

in size, in other words, are associated with differences in form, such as might be expected on the purely mechanical considerations underlying Ingold's proposition; the larger sporophores having relatively thicker stipes than the 'average type', and the smaller ones relatively more slender stipes.

The average dimensions for the different genera are of interest, and these are given in Fig. 2 (omitting genera represented by fewer than ten specimens). Rather surprisingly, it does not seem possible to generalize from these data as to the significance of the numerical size of the genus or of the character of the stipe, whether fleshy or cartilaginous. *Cortinarius* may be taken as an example of a large genus (128 measurements) in which, though the average dimensions for the genus are relatively far from the expected values, the data for the individual species still conform reasonably closely to the theoretical $y^3 \propto x^2$ relationship (Fig. 2, *inset*).

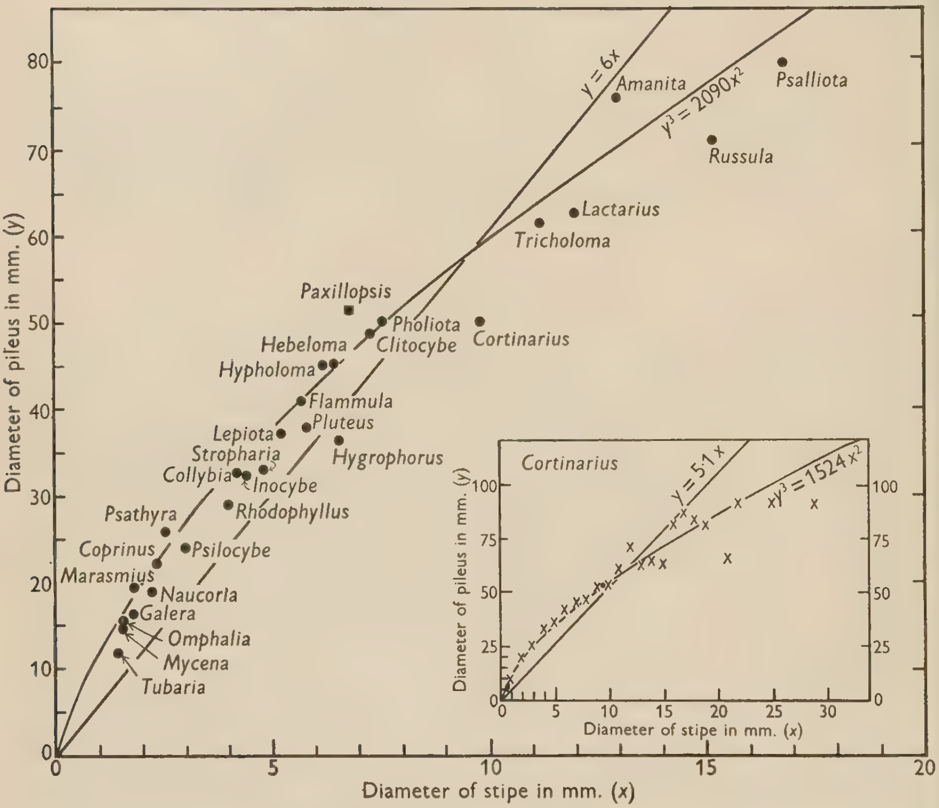

Fig. 2. Generic averages for pileus and stipe diameters, as in Fig. 1. *Inset*—diameters of pileus averaged against diameters of stipe; *Cortinarius* spp., 128 determinations. The solid circle indicates the geometric mean values.

The procedure of averaging pileus diameters against arbitrary arrays of stipe width, adopted for convenience following Ingold, appears to imply that stipe width is the independent variable; and the graphs have been arranged accordingly. Yet Ingold (1946, fig. 2) has expressed the relationship between these two variables, and arranged his graphs, the other way round, i.e. as if pileus diameter were the independent variable. This has not, however, vitiated the correctness of the conclusions drawn from his data, which are now fully confirmed. The inverse procedure, of averaging stipe widths against pileus diameters, allows of the same interpretation, though the agreement between the actual values and the computed curves is considerably lessened; doubtless, on account of the fact that the recorded dimensions of the pileus (2–178 mm.) vary much more widely than those of the stipe (1–32 mm.). A further biological justification for treating stipe width as the independent variable may be found by considering the development of the agaric sporophore, in which the stipe attains its full width long before the final expansion of the pileus.

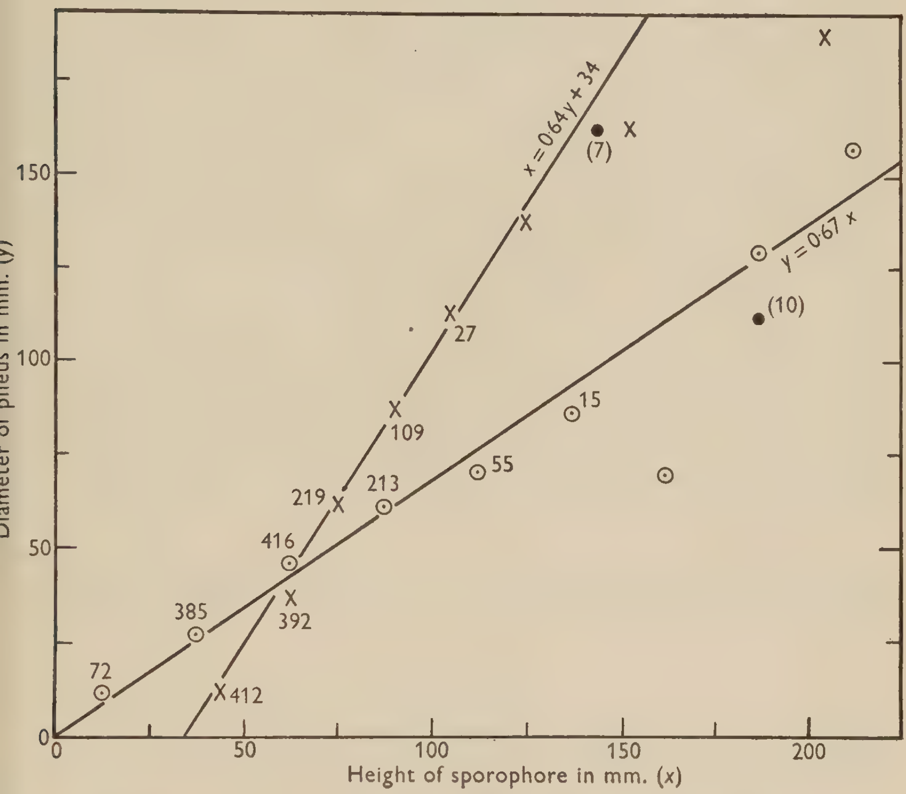

Fig. 3. Diameter of pileus and total height of sporophore; 1166 determinations. ⊙—⊙, diameters averaged against heights; ×—×, heights averaged against diameters. The figures refer to the number of determinations on which each point is based; the values for the last three points in each series (based on fewer than ten determinations) being combined, as shown by the solid circles.

CAP DIAMETER AND HEIGHT OF SPOROPHORE

The relationship is demonstrated graphically in Fig. 3. Averaging pileus diameters (y) for arrays of heights (x) at 25 mm. intervals gives a series of points lying very close to the straight line joining the origin with the point representing the 'average type' (pileus diameter 40·8 mm., height of sporophore 60·5 mm.). Such a relationship would suggest that the proportions of the two variables remain constant irrespective of the size of the fruit-body. On the other hand, averaging heights (x) for arrays of pileus diameters (y) gives points approximating to a straight line of the type $x = ky + c$; and that drawn in Fig. 3, again passing through the position of the 'average type', corresponds to $x = 0{\cdot}64y + 34{\cdot}0$ mm. Thus, Ingold's (1946) method of tabulation again appears to support the conclusion he drew from his own data, namely, that the proportions of the two variables do alter according to their size and that, with decreasing size, the height of the fruit-body tends to decrease towards an average minimum value of about 1·25 in. (34 mm.). The combined effect of the two methods of tabulation, as seen in the figure, is to suggest that the true relationship between size and height (midway between the lines plotted) is more nearly constant, with a theoretical minimum average height of the order of 0·75 in. (20 mm.). Again seeking a biological, ontogenetic parallel for this relationship, it may be noted that in the development of the individual fruit-body the final *elongation* of the stipe (as distinct from its increase in width) occurs almost simultaneously with the final expansion of the pileus.

The measurements on which this note is based were taken for me from Lange's illustrations by Miss S. E. Beckett to whom, with Miss A. T. Gardner, I am also indebted for assistance with their tabulation.

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OEDOCEPHALUM LINEATUM IS A CONIDIAL STAGE OF *FOMES ANNOSUS*

By B. K. BAKSHI

Forest Research Institute, Dehra Dun, India

(With Plate 7)

In dealing with the fungi associated with the ambrosia beetles in Great Britain (Bakshi, 1950), I described a new species, *Oedocephalum lineatum*, which was found in the galleries of *Trypodendron lineatum* infesting Japanese larch (*Larix kaempferi*). The conidiophores of the fungus developed abundantly in the tunnels. They were long and slender with apices swollen into heads on which conidia were borne on sterigmata. This type of secondary spore also formed in artificial culture of the fungus on malt agar. No other fruiting structures developed in the culture.

Recently Dr Findlay drew my attention to the similarity of the culture of the fungus with that of *Fomes annosus*. He had obtained a fructification of a member of the Polyporaceae (Pl. 7) in the culture of *Oedocephalum lineatum*. Dr Findlay also exposed blocks of Scots pine sapwood to the attack of *O. lineatum* for 4 months and found that, on the average, they lost 11·8 % of their dry weight showing that the fungus is definitely a wood-destroying species. He is therefore of opinion that *O. lineatum* is the conidial stage of *Fomes annosus*.

The conidiophore of *F. annosus* is oedocephaloid, like that of *Oedocephalum*. This type of secondary spore is characteristic of *Fomes annosus* in artificial culture, but is rarely found in nature. The abundant development of conidiophores (Bakshi, 1950, pl. 9, fig. 9) inside a gallery of the beetle is therefore noteworthy and is presumably due to high moisture within the tunnel. It may be mentioned that the logs infested by *Trypodendron lineatum*, in the galleries of which the fungus was found, had been felled and were in contact with the earth. No fructification of *Fomes annosus* developed on the host and the wood also did not show any rot. This therefore upholds my earlier view that the fungus is associated with *Trypodendron lineatum* and is introduced into the wood by the beetle.

Sincere thanks are due to Dr W. P. K. Findlay for the observations and for kind permission to publish the results along with the photograph.

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Bakshi, B. K. (1950). Fungi associated with ambrosia beetles in Great Britain. *Trans. Brit. mycol. Soc.* **33**, 111–120.

EXPLANATION OF PLATE 7

Fructification developed in culture of *Oedocephalum lineatum* on malt agar. (×5.)

(*Accepted for publication* 29 *October* 1951)

CAPNODIUM FOOTII AND *STRIGULA BABINGTONII*

By R. W. G. DENNIS

The Herbarium, Royal Botanic Gardens, Kew

AND M. B. ELLIS

Commonwealth Mycological Institute, Kew

(With 1 Text-figure)

Capnodium footii and *Strigula babingtonii*, described as two distinct organisms during the year 1849, are considered to be parts of one fungus for which the name *Chaetothyrium babingtonii* (Berk.) Dennis & M.B. Ellis is proposed, with *Strigula babingtonii* Berkeley, *C. footii* Berkeley & Desmazières, *Fumago fagi* Pers., and *Zukalia setosa* Woronichin as synonyms. The description given by Spegazzini of *Microxyphium footii*, taken by him as the type species of *Microxyphium*, is not based on authentic material.

In a paper entitled 'On some moulds referred by authors to Fumago, and on certain allied or analogous forms' Berkeley and Desmazières (1849) described *Capnodium footii* as follows: '*C. footii*, Berk. and Desm. Maculaeforme setulosum; peridiis subulatis simplicibus; mycelio subhyalino subgelatinoso. *Fumago fagi* Pers., Myc. Eur., Vol. 1, p. 10. *Microxiphium footii*, Harv. MSS. Extremely common on the leaves of evergreens, when it is often accompanied by *Strigula babingtonii*, and also on the leaves of deciduous trees as the Beech, and even on herbaceous plants, as *Mercurialis perennis*. Forming little, generally orbicular, thin patches, which under a microscope are setulose. Mycelium subgelatinous, readily imbibing water, subhyaline, when young subcontinuous, when old distinctly moniliform; the articulations elliptic, with one or two nuclei. Peridia dark, setiform, outer coat hyaline, the threads at first cylindrical, at length moniliform, hyaline, the ultimate joints breaking off; in some states the peridia are quite naked. They frequently, but not universally, spring from a little bulbous base. The fruit has not been observed in this species. Its discovery may warrant the formation of the genus *Microxiphium* Harv. It is scarcely probable that the asci in so narrow a space should be of the same nature as in other species. It occurs so frequently with *Strigula babingtonii* that it has been suggested that it bears the same relation to that species that *Tricharia* does to certain epiphyllous lichens. It is, however, found without any trace of the lichen and the lichen also occurs equally free from the bristly threads.' *Fumago fagi* Pers., cited as a synonym of *Capnodium footii*, was based by Persoon (1822) on a specimen from Mougeot and reference was made to its setae; no fruiting bodies were described. We have examined a specimen in Herb. R.B.G., Kew, labelled *Fumago fagi* which has, on the same sheet, drawings of the characteristic setae and notes in Mougeot's handwriting. There is no doubt that this is the same species as *Capnodium footii*. Fries (1832) cited *Fumago fagi* as a synonym of *Botrytis fumago*.

The name *Strigula babingtonii* was published by Berkeley (1849) a few months earlier than *Capnodium footii*. His description of this 'lichen' was as follows: 'Thallus yellowish fuliginous-olive when wet, much darker when dry, very thin and easily separating from the matrix, forming small irregular patches 2 or 3 lines or more broad on the upper and under surface of the leaves of Box, Laurel, *Phillyrea* and other evergreens, consisting of two distinct strata of which the inferior is composed of radiating, articulate or inarticulate variously branched irregular and sometimes moniliform filaments; the superior not always extending so far as the subjacent stratum and consisting of close packed minute cells, which usually have distinct endochrome. Perithecia globose above, but flattened below, cellular like the upper stratum, more or less collapsed above. Nucleus tinged with very pale red, consisting of delicate paraphyses and rather short, often very irregular asci, which are much constricted below, and contain subcymbiform, triseptate colourless sporidia.'

After examining a large number of herbarium specimens and fresh collections we have come to the conclusion that *Strigula babingtonii* and *Capnodium footii* are parts of the same fungus. Setae have been found in all the authentic collections of *Strigula babingtonii* which we have examined, even in those said by Berkeley to be 'without bristly threads', e.g. the collections from Hurstpierpoint in Sussex, and perithecia with asci and spores have been observed in collections authentic for the name *Capnodium footii*. Moreover, in sections it is seen that parts of the pellicle forming the outer walls of the perithecia are continuous with those bearing setae (Fig. 1*f*), and the mycelium in all collections is similar. Zahlbruckner (1922) stated that *Strigula babingtonii* was a fungus and both Hariot (1889) and Müller (1890) excluded it from the lichens. Leighton (1879) included it in his *Lichen Flora*, giving the spore measurements quite accurately as 0·018–0·023 by 0·005–0·007 mm. This fungus, originally described partly as a fungus and partly as a lichen, is redescribed below.

Colonies mostly epiphyllous, partly thin, grey and sparingly setose, partly black and densely setose, sometimes round and 0·5–4 mm. in diameter but often widely effused when they may cover almost the whole leaf surface; not forming leaf spots nor causing any discoloration of the host tissues. Mycelium superficial, forming a mat one or several layers of cells thick. This mat is composed partly of branched and anastomosing, subhyaline or pale olive, smooth-walled hyphae, 2–3 μ in diameter, which often lie at right angles to one another, and partly of a pellicle of round or oval, olivaceous cells, 3–6 μ in diameter which are usually darker around the bases of the setae (Fig. 1*a*). The transition from hyphal mat to pellicle is illustrated in Fig. 1*d*. Setae erect, straight or somewhat curved, sharply pointed at the apex, often swollen and bulbous at the base, 80–210 μ long, 6–8 μ wide immediately above the basal swelling, dark brown, opaque, often covered, except at the tip, by a layer of either subhyaline hyphae or olivaceous pellicle cells (Fig. 1*e*). Perithecia almost spherical, slightly flattened on top, often becoming concave on drying, olive to black, with a round pore at the apex, 90–210 μ in diameter; upper and side walls

30–50 μ thick, pseudo-parenchymatous, composed of several layers of cells, the inner layer subhyaline, the middle layers darker, the outermost layers derived from the mycelial pellicle (Fig. 1 *g*). Asci (Fig. 1 *c*) arising from the base of the perithecium, broadly cylindrical, rounded at the apex, narrowed at the base, 40–63 μ long, 13–17 μ wide, 8-spored with the spores usually in two rows. Ascospores (Fig. 1 *b*) broadly fusoid, sometimes slightly curved, rounded at the ends, hyaline, 3–6 septate, 14–23 by 5–7 μ. No true paraphyses seen. This fungus is clearly congeneric with *Chaetothyrium guaraniticum* Speg., the type species of *Chaetothyrium*, a detailed study of which was made by Bitancourt (1936) and we therefore propose the

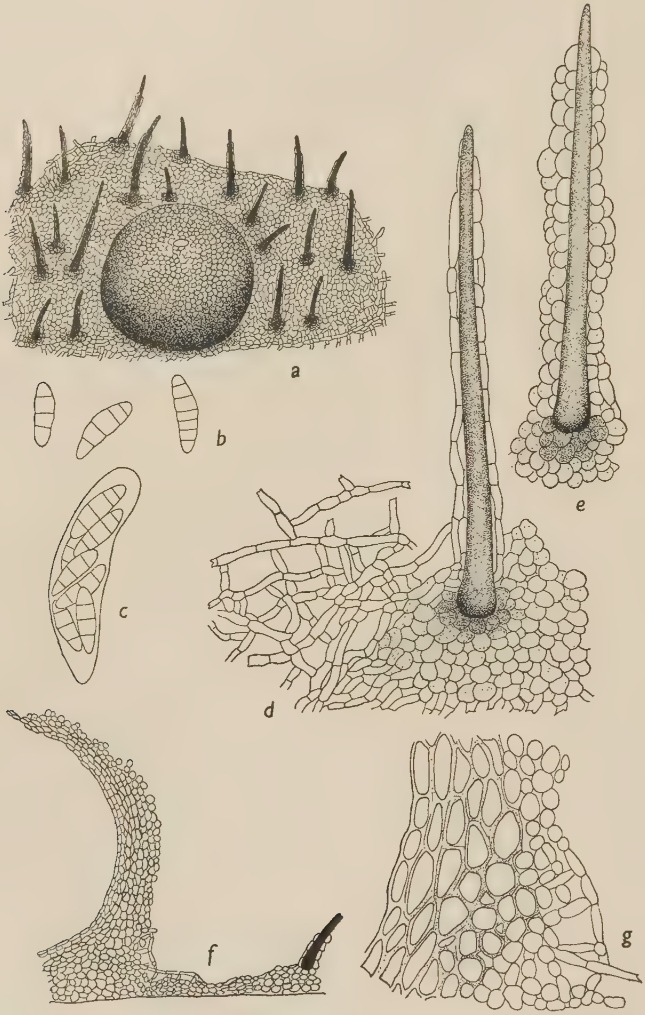

Fig. 1. *Chaetothyrium babingtonii*. *a*, part of thallus with perithecium and setae; *b*, spores; *c*, ascus; *d*, *e*, details of thallus and setae; *f*, section through perithecial wall and adjacent thallus; *g*, details of perithecial wall in section. *b–e* and *g*, × 500.

following new combination *C. babingtonii* (Berk. & Desm.) Dennis & M. B. Ellis. Hansford (1946) drew attention to the need for revision in this group of fungi and suggested a list of possible species of *Chaetothyrium*. He included *Zukalia setosa* Woronich. in this list. Woronichin (1915) did not see authentic material of *Capnodium footii* but thought that it might well prove to be the sterile mycelium of an organism extremely close to, if not identical with, his *Zukalia setosa*. A free translation of a paragraph near the end of his description of *Z. setosa* reads 'The identity of *C. footii* with *Z. setosa* can be established only by a study of the type specimen of the fungus Berkeley and Desmazières described, which was not available to me. For this reason I thought it better to consider my form as a new species.' Woronichin gave an excellent description of his fungus and there seems to be no doubt that his *Z. setosa* is the same fungus as *Chaetothyrium babingtonii*.

In their description of *Capnodium footii*, Berkeley and Desmazières refer to dark, setiform peridia and say 'it is scarcely probable that the asci in so narrow a space should be of the same nature as in other species'. These 'setiform peridia' are, in fact, mycelial setae which are frequently somewhat swollen at the base. References to *C. footii* are made by Cooke (1871, 1906), Smith (1884) and George and Ivy Massee (1913). Cooke (1871) says, with reference to the setae, 'Receptacles erect and bristle-like. Sporidia never found', and the Massees say, 'Perithecia? bristle-shaped, surrounded at the base by somewhat hyaline, moniliform threads, asci and spores unknown'. Saccardo (1882) placed *C. footii* under *Capnodium*, referring it to Section VIII *Microxyphium*, and saying of this section 'ascis ignotis; peritheciis subulatis'. Spegazzini made this species the type of the genus *Microxyphium* Sacc. em. Speg. and placed it in the Sphaeropsidales, giving the following generic description and citation. '*Microxyphium* Sacc. (Chr. em.): Biophilum superficiale; subiculum dematieum exhyphopodiatum; perithecia elongato-linearia sessilia simplicia v. ramosa, ostiolata, phaeochroma, sporulae continuae hyalinae v. chlorinae. *M. footii* (Berk. & Desm.) Harv. Sacc., l.c. 1 pg. 80 Typus.' We have seen nothing like this in any of the authentic material which we have examined and must assume that Spegazzini did not base his description on this fungus.

The following collections in Herb. R.B.G., Kew and Herb. I.M.I. have been examined. On *Arundinaria japonica*, Threeburrows, West Cornwall, March and April 1950, R. C. Congdon (comm. F. Rilstone). On *Buxus sempervirens*: Rushton, Northants, August 1848, M. J. Berkeley, in Herb. Borrer as *Strigula babingtonii* (cotype); same locality, undated, in Herb. Berk. as *Microxyphium footii* Harv. On *Eleagnus*, Threeburrows, West Cornwall, March and April 1950, R. C. Congdon (comm. F. Rilstone). On *Fagus sylvatica*, France, in Herb. Berk., apparently from Desmazières, labelled '*Microxyphium footii* Harv. in fagi, *Fumago fagi* Pers. Myc. Eur. 1 p. 10'. On *Ligustrum ovalifolium*, Kinloch, Isle of Rhum, July 1951, R. W. G. Dennis. On *Mercurialis perennis*, in Herb. Berk., H. O. Stephens, Bristol. On *Phillyrea*, Hurstpierpoint, Sussex, October 1848, leg. W. Mitten, in Herb. Borrer, as *Strigula babingtonii* (cotype). On *Prunus laurocerasus*: Ormesby, Cleveland, Yorkshire, 8 November 1853, W. Mudd; near Rokeby, Durham, W. Mudd and same locality April 1859, G. Dixon; Gopsall, Leicestershire, April 1850 and as Leighton Lich. Brit. Exs. 35, also in Herb. Berk as *Capnodium footii*; Cirencester, Gloucestershire, W. Joshua, January 1875; Cockfield, Suffolk, Labalestier Lich. Exs. 360, all as *Strigula babingtonii*; Rushton, Northants, Herb. Berk. as *Microxyphium footii*; Cambridge, Herb. Berk.; Twycross, Leicestershire, Cooke, *Fungi Brit. Exs.* II, 292; Highgate, London, 1871, Cooke, *Fungi Brit. Exs.* p. 595; Forden, Montgomeryshire, J. E. Vize, *Microfungi Brit.* p. 395; unlocalized, Rev. J. Gagliardi 1865, all as *Capnodium footii*; also an unlabelled collection, probably that cited in a letter from Dublin, D. Moore, 28 December 1844, attached to the same sheet. On *Rhododendron ponticum*, Vaynol Park, Bangor, North Wales, 12 September 1950, Noel Robertson.

A collection on *Camellia*, Cambridge, W. G. Smith in Herb. Cooke is a conidial fungus and, except for the one collection on *Fagus* from France cited above, all the other European material under the name *Camellia footii* examined by us has proved to be different from the type, viz. de Thümen Myc. Univ. 1291 on *Mercurialis*, 1944 on *Populus*; Roumeguère's 3096 on *Staphylea*, 5146 on *Yucca filamentosa*; Saccardo Myc. Ven. 1099 on *Hydrangea*; 1171 on *Cassinia*, and collections from Portugal on *Pelargonium* and *Psidium*.

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FIELD OBSERVATIONS ON THE SPREAD OF *ARMILLARIA MELLEA* IN APPLE ORCHARDS AND IN A BLACKCURRANT PLANTATION

By R. W. MARSH

Long Ashton Research Station, University of Bristol

(With 3 Text-figures)

Preliminary records of *Armillaria mellea* infections were made in a blackcurrant plantation from 1932 to 1941. These observations suggested that the major factor influencing the pattern of spread was root contact.

Recording of *A. mellea* infections was maintained from 1937 to 1951 in two Somerset farm orchards planted with standard apples of a wide range of ages and varieties. All the trees were on seedling stocks. No relation between susceptibility and environment or between susceptibility and variety was established. *A. mellea* killed very few of the trees under 15 years old, but in the 12 years 1940–51 the fungus killed approximately half of the trees aged over 30 years.

It is suggested that *A. mellea* infection of roots of apples on seedling stocks may be present for a number of years before it causes the death of the tree.

In 1925, Hendrickson published a plan illustrating the spread of *Armillaria mellea* during a period of 23 years in an orchard of plums and apricots in California. As there are no such records of the spread of *A. mellea* in fruit plantations in England the following observations are presented. The main records were made in two grass orchards of standard apples from 1938 to 1951: preliminary results were obtained between 1932 and 1941 in a plantation of blackcurrants.*

OBSERVATIONS ON BLACKCURRANTS

Records were made in a plot of Baldwin blackcurrants planted in 1927–8 at 6 ft. on the square. The site formed part of the plantations of the Long Ashton Research Station, and the soil, management and manuring of the plot were fully described by Wallace (1938). From 1935, cultivations were made only along the north-south alleyways.

The progress of infection by *A. mellea* is shown diagrammatically in Fig. 1. The first infected bush (labelled 0) was recorded in 1932: in 1933 infection spread to three adjacent bushes to the north and one to the east (labelled 1). Next year seven more bushes (labelled 2) became infected. At the end of 1934, an attempt was made to eradicate all diseased material from the area but although no new infection was seen in 1935, eleven bushes (labelled 4) became infected in 1936. The further course of infection can be followed in Fig. 1, the labels 5 to 9 representing the successive infections annually from 1937 to 1941. At the end of each season all obviously infected bushes were removed and in 1941-42 the whole plot was grubbed.

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* A paper on this subject was read by the author at the British Mycological Society's meeting at Bristol on 26 June 1943.

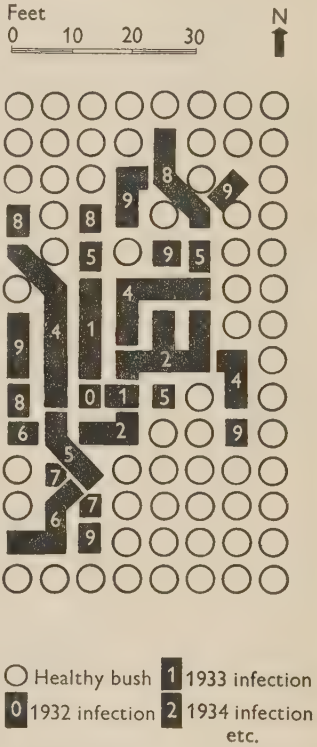

Fig. 1. Diagram illustrating spread of *A. mellea* in a blackcurrant plantation.

Fig. 1 clearly shows that infection did not spread outwards in concentric circles. The pattern of spread might rather be described as comprising tongues of new infection affecting up to five contiguous bushes, with a tendency to extend more rapidly in the north-south than in the east-west direction.

This suggests that the progress of the fungus through soil unoccupied by roots was slower than its extension by root contact. The tendency to quicker spread in the direction of cultivations may have resulted from the interference with root growth in the cultivated alleyways.

OBSERVATIONS IN APPLE ORCHARDS

The records on blackcurrants were taken on plants of the same variety and age, set out at an even planting distance. In contrast, the orchards used for the observations detailed below showed the irregular juxtaposition of apple trees of many varieties and ages which is a feature of most farm orchards in the west of England. The common occurrence of *A. mellea* in such orchards provided an unusual opportunity of recording the spread of the fungus in relation to age and variety of the host.

During 1938 four orchards in Somerset were selected for long-term recording and mapped by Mr J. E. Forshaw, Dr E. H. Wilkinson and the author. Recording on two of these sites lapsed during the 1939–45 war, but on the other two it was maintained annually until 1951. These two centres will be referred to below as the Taunton and Glastonbury orchards respectively. Both are grass orchards of standard apples on seedling stocks.

Sites and methods

The Taunton orchard. This orchard of approximately 100 × 80 yards, on a well-drained sandy loam contained, in 1938, 104 living trees and 18 dead trees and stumps. The planting distances varied between 16 ft. 6 in. and 31 ft. (see Fig. 2). The orchard included not fewer than twenty varieties (cider, culinary and dessert). The sorts most commonly represented—Morgan Sweet (21 trees), Kingston Black (12 trees) and Blenheim Orange (11 trees)—were generally distributed through the orchard. The tree ages ranged from 2 to approximately 80 years: a broad classification into age groups is given in Table 3.

The Glastonbury orchard. The Glastonbury orchard, 230 × 53 yards, lay on the margin of the Somerset 'moors', about 40 ft. above sea-level, on heavy soil with a high water-table. In 1938, it contained 157 living trees and 7 dead trees and stumps. The planting distance varied widely but was usually of the order of 20 ft. (see Fig. 3). The identified trees belonged to twelve varieties, the commonest being Red Jersey (24 trees) and Bramley (36 trees), both of which were distributed throughout the orchard. Most of the Bramleys were newly planted: otherwise the age distribution was similar to that in the Taunton orchard (see Table 3).

Method of recording. Records were ordinarily taken in September-October, when premature defoliation sometimes provided a guide to the presence of *Armillaria* infections. Any tree showing unthrifty foliage, an unusually leaning stem or a suspicious appearance of the bark at the butt of the trunk was carefully examined. Soil was removed to a depth of about 6 in. to bare the upper central portion of the main roots, which were then explored by incisions made into the cortex and wood. Usually it was not practicable to examine any part of the root system except that immediately adjoining the base of the trunk. Blackening of the host tissues was not recorded as an infection unless it was accompanied by the typical white fan-shaped mycelial plates of *A. mellea.* It frequently happened that there was a delay of 2 or 3 years between the first recording of infection and the death of the tree and, in this interim period, identification of the fungus could be confirmed by the presence of rhizomorphs and, occasionally, of sporophores.

Results

Yearly record of infections

Figs. 2 and 3 show the positions of each tree newly recorded as infected with *A. mellea* in each of the years 1938 to 1951, except 1950. The yearly record for the two orchards is summarized in Table 1.

Table 1. *Numbers of trees newly infected with* Armillaria mellea

	1938	'39	'40	'41	'42	'43	'44	'45	'46	'47	'48	'49	'51	Total
Taunton	16	9	1	2	0	3	1	1	0	1	1	6	1	42
Glastonbury	10	2	0	3	0	2	4	0	5	1	3	6	9	45

The infections credited to 1938 include a number of dead trees and stumps representing the accumulated effect of the attacks for several years immediately preceding the first (1938) recording. In the Taunton orchard, in particular, such attacks largely account for the patch of infection shown in Fig. 2 near the eastern side of the orchard. The 1939 figures may also include some infections that should have been recorded in 1938 but were overlooked. After 1939, it is thought probable that the figures fairly indicate the progress of infection in the preceding 12 months. In Figs. 2 and 3 the infections existing more than 10 years before these diagrams were drawn (in 1951) are emphasized by being shown in white on a black background.

Table 1 gives no consistent evidence of seasonal effect, when the two orchards are considered together: neither does it indicate that the wetter Glastonbury site exhibits any outstandingly greater liability to *A. mellea* infection than the Taunton orchard.

Susceptibility of varieties

A detailed statement of infections classified under varieties is not given, since the results so far obtained show no indication of significant differences in varietal susceptibility. For example, in the Taunton orchard, the trees of Morgan Sweet, making up 17% of the orchard population, have given 13% of the infections: in the Glastonbury orchard 15% of the trees are of

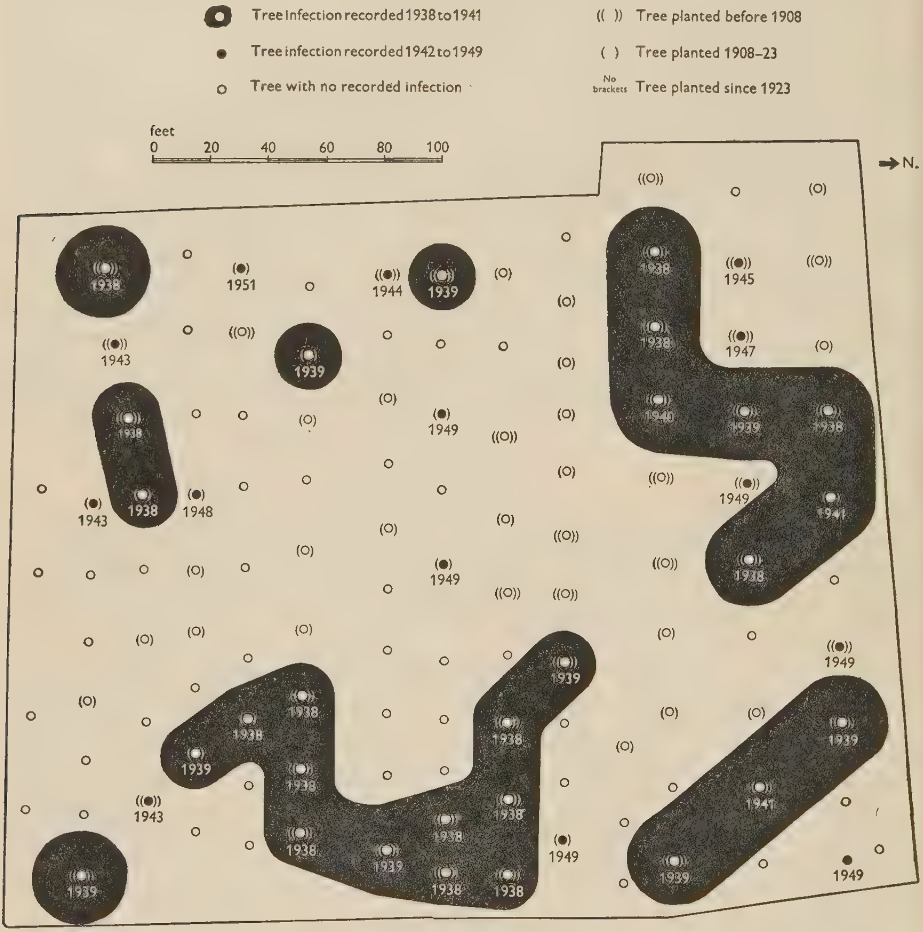
Tree infection recorded 1938 to 1941
Tree infection recorded 1942 to 1949
Tree with no recorded infection
(( )) Tree planted before 1908
( ) Tree planted 1908–23
No brackets Tree planted since 1923
feet
0
20
40
60
80
100
N.

Fig. 2. Plan of Taunton orchard.

Table 2. *Effect of proximity to existing infections*

Orchard	Distance from tree infected 1938–9 (ft.)	Total trees in 1939	Total infections 1940–51
Taunton	Under 35	65	12
	35–70	29	5
	Over 70	Nil	Nil
Glastonbury	Under 35	49	11
	35–70	67	20
	Over 70	32	2

the variety Red Jersey and this variety accounts for 17% of the infections. The apparent anomaly is provided by the Bramley trees at Glastonbury, which form 22?% of the population but have contributed only 3% to the casualties. However, as already stated, these are almost all young trees, and this, as shown below, is a factor of over-riding importance.

Effect of proximity to existing infections

The orchard plans (Figs. 2, 3) show that new infections are more common in the vicinity of previous attacks, although the relationship between infection and proximity is obviously not clear-cut. Taking the 1939 orchard population and setting out, arbitrarily, zones of 35 and 70 ft. from the infections then existing, the totals of trees in these zones that became infected in the ensuing 12 years are as shown in Table 2.

In the Taunton orchard all the trees were within 70 ft. of a 1938–9 infection. The figures from Glastonbury suggest a marked falling-off in infection beyond the 70 ft. range, but none of the records indicates that liability to attack in the 0–35 ft. circle was higher than in the 35–70 ft. zone.

Effect of tree age

Exact figures for tree age could not be obtained, but, in the 1938 survey, the three observers drew up an agreed list classifying each tree into one of three age categories: under 15 years, 15–30 years and over 30 years.

The incidence of *Armillaria* attack on trees of these three categories is summarized in Table 3. Under the heading 'Records 1938–9', the numbers of trees and of infected trees at the outset of the observations are assembled. The fate of the trees not recorded as infected in 1939 is followed in the remaining columns. (Because of the proximity effect shown in Table 2, the trees more than 70 ft. from an original infection are shown separately.)

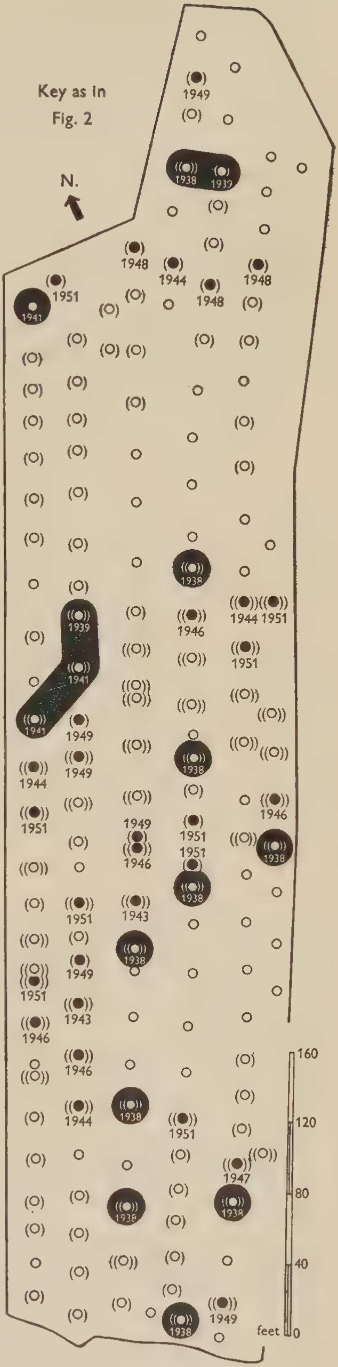

Fig. 3. Plan of Glastonbury orchard.

Table 3 clearly indicates the effect of tree age on liability to infection. Of the tree population of 1938, those planted after 1923 have shown only 2% deaths compared with approximately 60% for the old trees. In the trees of medium age, the figure for the Glastonbury orchard is probably affected by the factor of distance from sources of infection, but even so it is over 20%. If the records of 1938–9 are omitted, those of the succeeding 12 years still show over half of the old trees becoming infected compared with 2/94 of the young trees and 19/93 of the intermediate group.

Table 3 is incomplete in that it does not include trees planted since 1938 as replacements for those killed by *A. mellea*. In all, twenty-two such re-fills have been planted in the Glastonbury orchard and thirteen at Taunton. Although most of these young trees have been set out on the stations from which *Armillaria*-infested trees have been uprooted, not one has up to the present been recorded as attacked by *A. mellea*.

Table 3. *Summary of records of* Armillaria mellea *infections in relation to age of tree*

		Records 1938–9		Records 1940–51				
				Trees < 70 ft. from 1938–9 infection		Trees > 70 ft. from 1938–9 infection		
Orchard	Tree planting date	No. of trees	Infections recorded	No. of trees	Infections recorded	No. of trees	Infections recorded	Total all infections
Taunton	Before 1908	37	**20**	17	**9**	—	—	**29**
	1908–23	33	**5**	28	**7**	—	—	**12**
	1923–38	49	**0**	49	**1**	—	—	**1**
	Totals	119	**25**	94	**17**	—	—	**42**
Glastonbury	Before 1908	48	**10**	35	**19**	3	**1**	**30**
	1908–23	67	**2**	44	**12**	21	**0**	**14**
	1923–38	45	**0**	37	**0**	8	**1**	**1**
	Totals	160	**12**	116	**31**	32	**2**	**45**

Discussion

Neither the blackcurrant nor the apple records support the hypothesis that the growth of rhizomorphs in soil unoccupied by roots is a major factor in determining the pattern of spread of *A. mellea*.

The progress of infection in the blackcurrant plot from 1932 to 1941 could reasonably be explained by assuming that the fungus spread from bush to bush by root contact, and that it could invade the root system of a blackcurrant sufficiently quickly to bring about death of the entire bush in the season of initial infection.

The observations in the Taunton and Glastonbury apple orchards were severely restricted by the inaccessibility of most of the tree roots. At these sites, a tree could not be listed as infected until the fungus mycelium had reached the trunk. Numerous examples were recorded in which infection was first noted in one segment of the base of the trunk, but complete encirclement required a further 2 or 3 years. This slow progress of the fungus in the tissues suggests that in these trees an invasion of the peripheral portions of the root system might precede by some years the recognition of visible symptoms of attack at the base of the trunk.

The apparent lack of any consistent pattern of spread in the infections in the Somerset orchards might therefore result from differences in the rate of root invasion of individual trees adjoining an infected site. In conifers, variation in resistance to *A. mellea* has been recorded by Day (1929), but he suggested that external factors were of more significance than inherent qualities of the host. In the Taunton and Glastonbury orchards, however, the rarity of trunk infection in the young apples, and its much more frequent occurrence in the older trees in the same environment, suggest the hypothesis that the invasion of seedling apple roots is a gradual process in which the balance in favour of *A. mellea* increases as the vigour of the tree declines. In the younger tree, the normal development of new roots may compensate for the damage inflicted by *Armillaria* invasion; as the tree matures it appears that the fungus gains the ascendancy; and in trees over 30 years old there is a high probability that *Armillaria* infection of the roots will spread to the base of the trunk and bring about death of the tree by girdling.

It must be emphasized that the ages cited in the preceding paragraph are those of apple trees on seedling stocks, which have normally a profitable life of approximately 70 years (Barker, 1937). In commercial plantations of dessert or culinary apples on vegetatively propagated semi-dwarfing stocks the life cycle is shorter and, on such stocks, trees not more than 10 years old may be killed by *A. mellea*.

Because of the potential longevity of the standard apple tree, the losses due to *A. mellea* attack remain of serious economic importance, even if the tolerance to infection of the younger trees proves to be of general occurrence. In considering the possibility of assessing the results of control measures in such orchards, the observations given in this paper may serve as a warning that the incidence of individual new infections of *A. mellea* in relation to those already charted cannot be certainly predicted and, consequently, claims for the beneficial effects of trenches or similar barriers may be difficult to substantiate.

In selecting the sites for observation and in the initial mapping and recording of the farm orchards invaluable assistance was given by Mr J. E. Forshaw (then Instructor in Cider Orcharding for Somerset) and by Dr E. H. Wilkinson. In subsequent recording, the help of Mr S. H. Crowdy, Dr R. S. Willison and Mr A. H. Fielding is gratefully acknowledged.

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GRAMINICOLOUS PYRENOMYCETES

IV. *MICROTHYRIUM NIGRO-ANNULATUM* N.SP. AND *M. GRAMINEUM*

By JOHN WEBSTER

Department of Botany, University of Sheffield

(With 3 Text-figures)

Microthyrium nigro-annulatum n.sp. on *Dactylis glomerata* is described. It is compared with *M. gramineum* on *Psamma* which occurs in Britain, but has not apparently been recorded hitherto. *M. gramineum* var. *major* Grove is rejected as a *nomen confusum.*

Recent studies (Robertson, 1950; Ellis, 1951; Godwin & Andrew, 1951; Webster, 1951), have shown that members of the Microthyriaceae are more common in Britain than had previously been supposed. The purpose of this paper is to record two further species.

Microthyrium nigro-annulatum sp.nov.

Mycelium superficiale, ramosum, septatum, hyalinum, ex hyphis circa 4 μ latis compositum. Thyriothecia sparsa, vel grisea vel nigra, centro distincte fusciore, tereta et forma circularia, 54–90 μ. Membrana superior ex cellulis paene quadratis composita, quae margine sunt circa 4 μ latae, centro angustiores; ostiolum numero cellularum parvarum et fusciorum circumdatum. Asci numerosi, sessiles, obclavati, octospori, $20–26 \times 6–8\ \mu$. Ascosporae inordinate juxta basem asci dispositae, hyalinae, utrimque acutae, bicellulares (aut nonnumquam continuae), septo transverso in duas partes iniquas divisae, cellula superiore paulo majore; 2–3 guttulis, $6{\cdot}5–10{\cdot}5 \times 1{\cdot}5–2{\cdot}5\ \mu$. Paraphyses non visae.

In culmis vaginisque *Dactylidis glomeratae*, Fulwood, prope Sheffield, Anglia. Specimen No. 1041 Mycological Herbarium of the University of Sheffield, quod typus est, in Herbario, Horti Botanici, Kew retinetur.

In studying the microfungi on *Dactylis* culms a small *Microthyrium* was encountered. A study of the literature failed to reveal any description which matched this fungus which is accordingly described as new, under the name *M. nigro-annulatum.* The fungus occurs on stems and leaf-sheaths of *Dactylis* towards the base of the inflorescences, both of the current and of the previous season, whilst these are still erect or after they have fallen on to the surface of the ground. The thyriothecia are scarcely visible to the naked eye, but are readily observed under a dissecting microscope. Preparations were made by the cellulose acetate technique (Ellis, 1950) and also by removing thyriothecia directly with a sharp scalpel in order to crush them to reveal asci and ascospores. The preparations were mounted in lactic acid and heated gently.

The mycelium is superficial, branched, septate, hyaline, and made up of hyphae about 4 μ wide. The thyriothecia are scattered, grey to black in colour with a distinct darker centre, smooth and circular in outline, 54–90 μ in diameter (thirty measured). The wall of the covering membrane is made up of radiating files of roughly square-shaped cells about 4 μ wide at the margin, and narrower at the centre. The ostiole is surrounded by a ring of small cells with thick black walls; these cells are frequently turned outwards to form a reflexed rim around the opening (Fig. 1 A, B). The asci are numerous (up to twenty ripe asci have been observed in a thyriothecium), sessile, obclavate, wider at the base, tapering towards the apex, 8-spored, 20–26 × 6–8 μ (thirty-five measured in lactic acid). The ascospores, arranged irregularly near the base of the ascus, are usually 2-celled, with a single transverse septum dividing the spore into two unequal portions, not or slightly constricted at the septum, wider at the middle, tapering towards the pointed ends, hyaline, with two to three guttules, 6·5–10·5 × 1·5–2·5 μ (twenty measured in lactic acid) (Fig. 1 C). Occasional unicellular spores were observed. Paraphyses were not seen.

This description was drawn up from a collection made at Fulwood, near Sheffield, on 3 January 1951 (Herb. Sheffield No. 1041). This specimen is now in the Herbarium, Royal Botanic Gardens, Kew. Various other collections have been taken from this locality, from Annesley Park, Nottinghamshire, and from Lindrick Common, near Worksop, Nottinghamshire. In all these places the fungus flora of the *Dactylis* culms has been studied intensively, and I suggest that similar studies elsewhere would show that the fungus is common and widely distributed. It occurs throughout the year, and is most commonly found on the basal internodes and leaf sheaths.

Microthyrium gramineum Bomm., Rouss. & Sacc.

Microthyrium gramineum Bomm., Rouss. & Sacc., described from leaves of *Psamma arenaria* in Belgium (Saccardo, 1891), has rather similar dimensions to *Microthyrium nigro-annulatum*, and it was felt desirable to compare these two fungi. I have examined the type specimen of *M. gramineum*. The specimen is labelled 'Herb. E. Bommer & M. Rousseau, Microthyrium gramineum, Bom. Rous, Sac. Sur les Ammophila arenaria, Le Coq. 1892. Sept. leg. M. Rousseau' and marked 'type' in red ink.

The specimen consists of one piece of a leaf of *Psamma arenaria*. On the outer surface are numerous thyriothecia. A few thyriothecia were removed as previously described. The fungus matches fairly closely the original description. It is, however, briefly re-described here in order to compare it with *Microthyrium nigro-annulatum*. The mycelium is superficial, pale brown, branched, and septate, and composed of hyphae 2–3 μ in width. The thyriothecia are scattered or confluent and develop on the superficial mycelium; ten thyriothecia in lactic acid measured 60–130 μ in diameter (70–90 μ in the original description). The covering membrane is composed of radiating files of brown, irregularly shaped cells, 4–14 μ measured in a radial direction and 2–6 μ tangentially, at the outer edge projecting irregularly to form a fimbriate margin, at the centre breaking down to form an irregular ostiole 6–10 μ in diameter, roughly circular, but occasionally opening by means of stellate cracks (Fig. 2 A). The thyriothecia contain up to about fifteen ripe asci. The asci are obclavate or elliptical, broadest at the base and tapering to the rounded apex, outer and

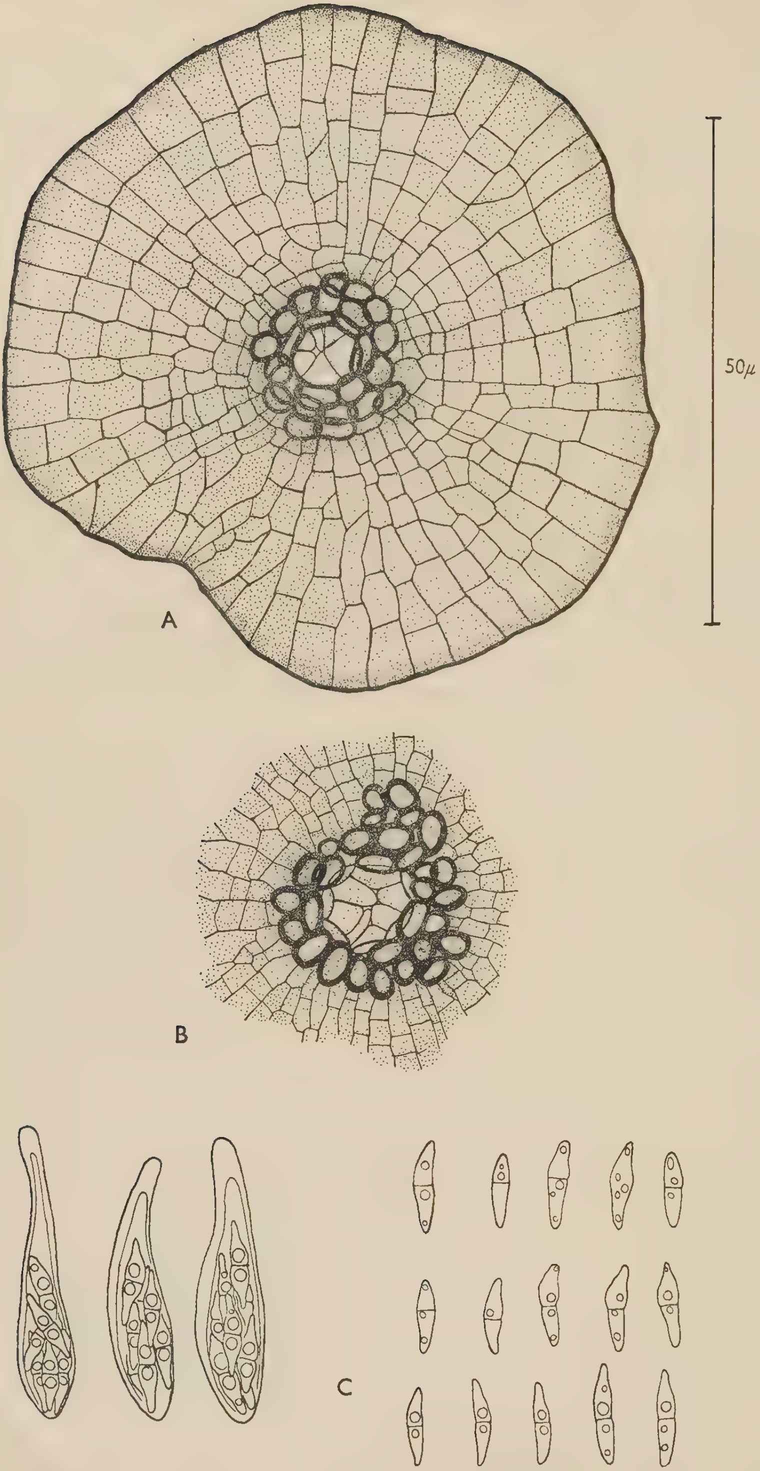

Fig. 1. *Microthyrium nigro-annulatum*. A, thyriothecium showing the smooth margin; B, ostiole of thyriothecium showing the ring of black, thick-walled cells; C, asci and ascospores.

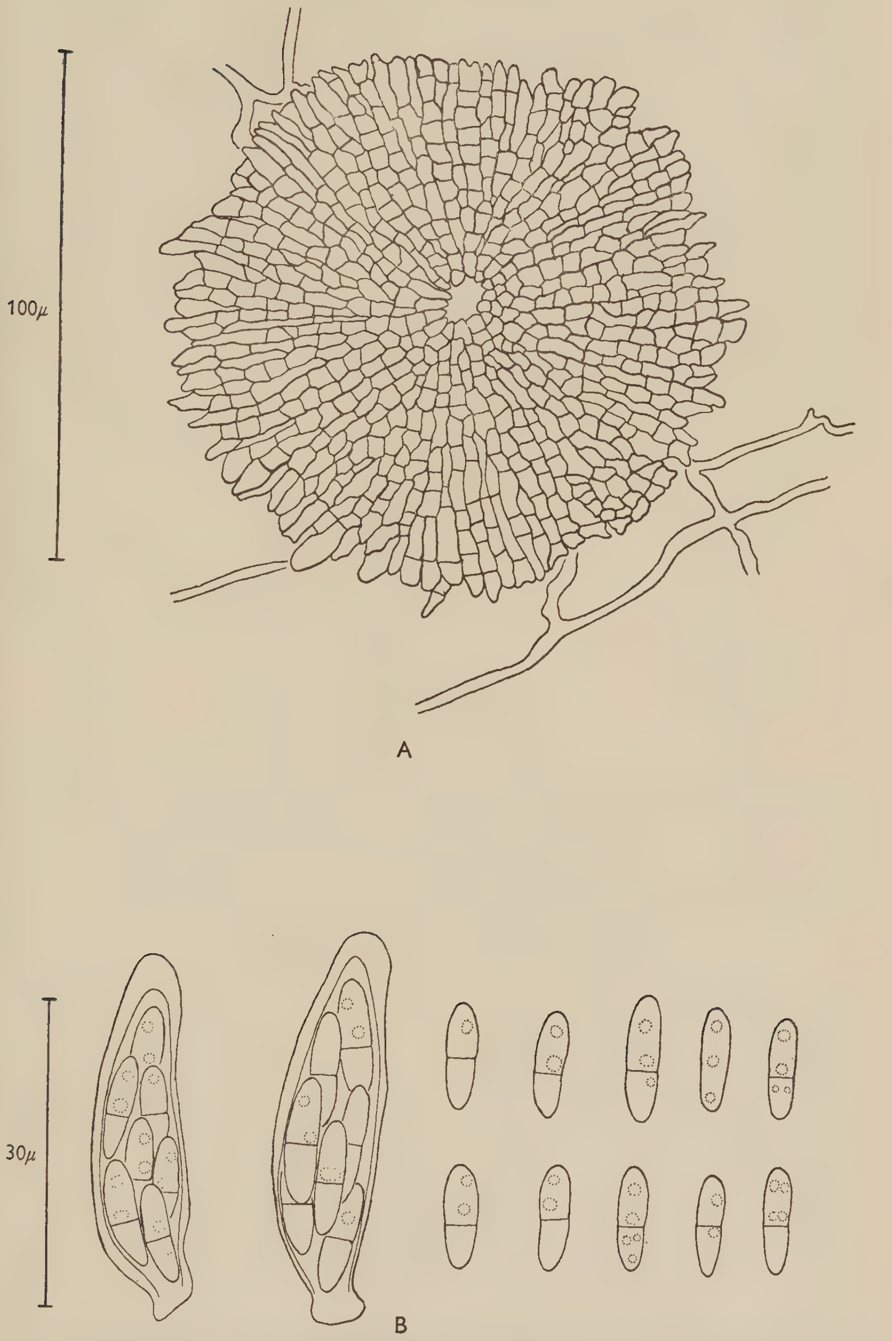

Fig. 2. *Microthyrium gramineum.* A, thyriothecium showing the fimbriate margin; B, asci and ascospores. (From the type specimen.)

inner membranes clearly distinguishable, 8-spored; twenty asci in lactic acid measured 26–37 × 8–10 μ (27–30 × 7·5–10 μ in the original description) (Fig. 2B). The ascospores are multiseriate, 1-septate, hyaline, with several small guttules, cylindrical with rounded ends; the lower cell is usually rather shorter and tapers towards the end; twenty ascospores in lactic acid measured 9–12 × 3–3·5 μ (9 × 3 μ in the original description).

The two fungi are clearly distinguishable. The margin of the thyriothecium is smooth in *M. nigro-annulatum* and fimbriate in *M. gramineum*; and the structure of the ostiole is also different in these two fungi.

Grove (1933) described *M. gramineum* var. *major* on dead leaves of *Psamma arenaria* collected at Sandwich Bay, Kent, August 1929. I have examined this and various other specimens of *Microthyrium* on *Psamma* from Grove's Herbarium in the University of Birmingham. These specimens, together with two of my own collections, are annotated below.

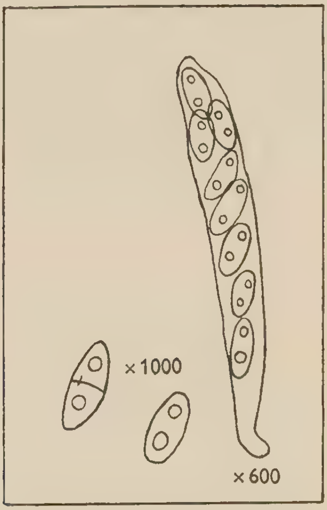

Fig. 3. The drawing enclosed with Grove's specimen (no. 1 in this paper) reproduced to the same size as the original.

(1) Specimen from Grove's Herbarium labelled '*Microthyrium gramineum* B.R.S. and *M. psamminum* sp.n. on *Psamma arenaria*, Sandwich Bay Kent, Aug. 1929'.

This is presumably the material from which *M. gramineum* var. *major* was described. The packet contains a small piece of paper with drawings in pencil (Fig. 3). On one side is a drawing labelled 'margin × 1000', and on the other a single ascus labelled '× 600' and two spores labelled '× 1000'. From the stated magnification this ascus is calculated to measure 90 × 11·6 μ, and the free ascospores 12 × 5 μ and 10 × 4·5 μ. The description refers to perithecia 300–400 μ in diameter, containing asci 70–80 × 7–8 μ, with spores 14–15 × 4–5 μ, doubtfully 1-septate, and with abundant paraphyses. Examination of the specimen has failed to reveal a *Microthyrium* with these dimensions. However, a few thyriothecia which agree in all respects with the type specimen of *M. gramineum* were found after careful searching with a dissecting microscope, as was originally observed by Grove. The dimensions of these thyriothecia, with their asci and spores, are compared in Table 1 with those obtained from the type specimen. It seems possible from the labelling of the herbarium packet that Grove noted that there were two species present on the *Psamma* leaves, *Microthyrium gramineum* Bomm., Rouss. & Sacc., and a second species which he may have intended to publish under the name *M. psamminum*. Later he presumably decided to use the name *M. gramineum* var. *major* for this second form. When, however, this name was published no mention was made of the occurrence of typical material of *M. gramineum*. The absence of material of *M. gramineum* var. *major* on the Sandwich Bay specimen is somewhat disturbing. Growing on the *Psamma* leaves with *Microthyrium gramineum* are the apothecia of a Discomycete identified by Dr R. W. G. Dennis as *Mollisia arenevaga* (Desm.) Phillips. The apothecia measure up to 450 μ in diameter, with asci 70–86 × 10–13 μ, abundant paraphyses and ascospores measuring 12–15 × 4–6 μ. It will be noted that the dimensions of this fungus agree (apart from the ascus width) with those given for *Microthyrium gramineum* var. *major*. However, the calculated width of the ascus drawn by Grove is 11·6 μ. It seems possible that in mounting the *M. gramineum* an apothecium of the Discomycete may have been included and led to confusion. This view is supported by Grove's drawing which is beyond doubt made from an ascus of the *Mollisia*. Dr Dennis (personal communication) writes 'Grove's figures are surely those of the *Mollisia*'. In the circumstances I feel that there is considerable doubt about the status of *Microthyrium gramineum* var. *major* and propose that it be rejected as a *nomen confusum*.

Table 1. *Measurements of ten thyriothecia, twenty asci and twenty ascospores of four specimens of* Microthyrium gramineum

Specimen	Thyriothecia (size in μ)	Asci (size in μ)	Ascospores (size in μ)
Type	60–130	26–37 × 8–10	9–12 × 3–3·5
1	76–100	26–30 × 9–10	9–10 × 2·5–3
3	90–140	30–34 × 8–10	9·5–10·5 × 3–3·5
4	70–110	20–28 × 9–11	9·5–10·5 × 3

(2) Specimen from Grove's Herbarium labelled '*Microthyrium psamminum* B.R. & S. on *Psamma*, Perranporth, Cornw. Sept.'.

The specimen consists of a small portion of a leaf of *Psamma* with thyriothecia of *Microthyrium gramineum*. Within the packet is a drawing of a thyriothecium. The drawing is labelled 'Microthyrium on Psamma × 300 2/9/29'.

I cannot trace the publication of the name *M. psamminum* (it is not listed in Stevens & Ryan, 1939). Grove probably used the epithet '*psamminum*' in error for '*gramineum*'.

(3) A third specimen from Grove's Herbarium is presumably part of the same collection; it is labelled 'Microthyrium Psamma ammophila, Perranporth, W. Cornwall, F. Rilstone 2/9/1929'.

In pencil on the packet is a drawing of a thyriothecium, an ascospore and the remarks 'no spores seen'. This is also typical material of

M. gramineum. Measurements of thyriothecia, asci and ascospores are presented in Table 1.

(4) Two collections by the writer on *Psamma arenaria* at Rhosneigr, Anglesey, 21 March 1951, and at Spurn Point, Yorkshire, 22 July 1951, are also referred to *Microthyrium gramineum.* A portion of the former collection has been sent to the Herbarium of the Royal Botanic Gardens, Kew, and its measurements are included in Table 1.

Further collections will probably reveal that *M. gramineum* is widely distributed on *Psamma* in Britain.

I wish to accord my sincere thanks to Dr W. B. Robyns of the Botanic Gardens, Brussels, and Dr C. J. Hickman for their kindness in sending specimens, and to Dr R. W. G. Dennis for identifying the Discomycete. I am indebted to Mr A. O. Hulton for the Latin diagnosis. This work was in part financed by a grant from the University of Sheffield Research Fund.

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THE FUNGUS FLORA OF COMPOSTS

By D. JEAN EASTWOOD

(*Macaulay Institute for Soil Research, Craigiebuckler, Aberdeen*)

Quantitative determinations of fungi in composts of fresh lawn mowings and barley straw have shown that these organisms are destroyed in the centre of both kinds of compost by the high temperature which develops. After the high temperature phase, greater development of fungi occurs in the straw compost. It is thought that adverse physical and chemical conditions limit their development in grass composts.

Some of the fungi carried by the material initially survive round the edges of the compost and persist during the period of composting. In the straw composts, the cellulose decomposers become particularly active.

Little work has been done on the microbiological aspects of composting. Webley (1947*a*, *b*; 1948) and Forsyth and Webley (1948) made a start with the aerobic mesophilic and aerobic thermophilic bacterial floras. This paper is an attempt to study the fungus flora of composts along similar lines.

Two types of material were separately composted and studied, viz. fresh young grass cuttings (lawn mowings) and cut barley straw. Owing to the low nitrogen content of the latter, ammonium nitrate was added to make up the total nitrogen to that specified by Hutchinson & Richards (1921) for the 'Adco' process. No treatment of any kind was given to the grass cuttings.

The compost container and technique of composting used were the same as those described by Webley (1947*b*), and the reader is referred to that paper for full details.

OBSERVATIONS ON BEHAVIOUR OF MATERIAL, MOISTURE CONTENT, TEMPERATURE AND pH DURING THE COMPOSTING PERIOD

These were similar to the results recorded in the previous work (Webley, 1947*b*). In order to maintain the unity of the present paper, some details are given below.

The grass cuttings compacted rapidly, sinking half-way down the container in 2 days, and to within 8 in. of the bottom after 22 days. The straw compacted less readily, and after 100 days had sunk only half-way down the container.

Determinations of moisture content were made on samples taken from the centre, and were calculated as a percentage of the oven-dried material. Little variation occurred throughout a compost, the moisture content being from 80 to 85 % in both types during 90 days.

A high temperature phase was characteristic of both types of compost. The grass rose to the maximum of 65° C. in 2 days, whilst the straw attained a temperature of the same order after 4–6 days. Both had fallen to the temperature of the air by about the twentieth day.

Changes in the pH of the material are recorded in Table 1. The composting grass developed and maintained greater alkalinity than did the straw. It appears that the thermophilic bacterial flora, which develops during the high-temperature phase, attacks the organic nitrogenous material of the grass, liberating ammonia, and thus accounting for the higher pH values (Webley, 1947*a*; Forsyth & Webley, 1948).

Table 1. pH *of compost material*

Grass compost		Straw compost	
Days of composting	pH	Days of composting	pH
0	6·26	0	6·66
5	8·35	5	6·5
26	7·64	20	7·05
58	8·6	42	7·0
90	8·64	88	5·4

QUANTITATIVE MYCOLOGICAL OBSERVATIONS

All samples were taken from the central region of the composting mass. At each sampling, material was removed by hand (previously sterilized with 70 % alcohol), thus exposing the centre of the mass. Pieces of grass or straw were then withdrawn at random from this region by means of sterile forceps, and transferred to a sterile container. The disturbed material was then replaced, as nearly as possible, in its original position.

The dilution-plate method for estimating numbers of fungi in soil, as standardized by Brierley, Jewson and Brierley (1928), was adopted for quantitative determinations of fungi in the composts. Waksman's dextrose-peptone medium, acidified to pH 4·8, was selected from a range of media for plating since it yielded the highest counts (222,000–235,000 fungi/g. of fresh lawn mowings). The same medium incorporating Rose Bengal as a bacteriostatic agent, as recommended by Smith and Dawson (1944), did not compare favourably with the acidified medium (5000–75,000 fungi/g. of fresh lawn mowings).

Colonies were generally smaller on the Rose Bengal medium and species of *Mucor* did not appear, whereas they developed frequently on the acidified medium without Rose Bengal. No other qualitative differences between fungi developing on the range of media investigated were apparent.

Plates of Waksman's acid medium and the Rose Bengal medium, prepared during the high-temperature phase of the composts, were incubated at 60° C. to detect the presence of thermophilic fungi. Otherwise incubation was carried out at 25° C.

One of the limitations of the dilution technique is that it makes no distinction between fungal mycelium and spores. It has been suggested by McLennan (1928), that by subjecting soil to vacuum desiccation it is possible to destroy fungal mycelium leaving spores unaffected. Such a treatment would prove a useful adjunct to the dilution technique. In testing the technique on fungi in pure culture however, I have found that whilst mycelium was destroyed by a period of 3 days' desiccation (as recommended by McLennan), there was also a reduction of about 25 % in the percentage of spores surviving. It was therefore considered that the technique was not sufficiently critical to warrant its adoption as a routine procedure, and it was not employed as such in this work.

The results in Table 2 are representative of determinations made on several composts of each type.

Since there was no development of fungi on the plates prepared during the high-temperature phase, it can be assumed that at this stage the fungi at the centre of the composting mass were destroyed. No evidence of thermophilic fungi was found in either compost. After the high-temperature phase, larger numbers of organisms were found in the straw than in the grass. This result confirmed the visual observation of greater fungal development of the straw.

Table 2. *Numbers of fungi/g. compost material*

Grass compost			Straw compost		
Days of composting	Temperature at centre compost (° C.)	Nos. of fungi/g. fresh material	Days of composting	Temperature at centre compost (° C.)	Nos. of fresh fungi/g. material
0	16	201,000	0	20	89,000
3	65	0	5	64	0
8	48	0	10	36	0
13	27	0	20	20	86,000
26	15	47,000	31	14	25,300,000
34*	15	40,000	38*	—	—
48	13	10,000	48	14	5,500,000
64	10	8,000	77	21	5,233,000

* At this stage the compost was turned.

Qualitative mycological observations

For identification, isolations of fungi were made from dilution plates and from plates inoculated directly with material taken from the centre and other regions of the composts. Microscopic examination of samples was also made.

Tables 3 and 4 summarize observations on a grass and straw compost respectively and are characteristic of each type.

In the grass compost, by the fifth day, the cuttings at the centre had become brown and slimy. By the eighth day mycelial development was seen to extend about 3 in. into the mass from the edges. At this stage, microscopic examination confirmed the presence of fungal mycelium around cuttings from the sides of the compost and occasional conidiophores of *Penicillium* were observed. By the twenty-sixth day the cuttings had compacted and nematodes were abundant and interfered with the isolation of organisms, particularly in samples from the edges of the compost.

In the straw compost fungal development was obviously greater than in the grass and some organisms became strikingly dominant.

Chaetomium globosum produced perithecia in abundance over the surface of the straws throughout the compost. On the tenth day of composting, samples were taken at three points, each 4 in. from the edge of the compost and 6 in. below the surface. Straws were selected at random from each sample and examined microscopically. The occurrence of recognizable organisms on a total of sixty straws is recorded in Table 5.

Colonies of *Aspergillus fumigatus*, *A. terreus*, *Monotospora* sp., *Trichoderma viride* and *Chaetomium globosum* always appeared on dilution plates.

Table 3. *Fungi isolated from grass compost*

Centre of compost		Side of compost (3 in. from edge and 6 in. below surface)	
Days of composting	Fungi isolated	Days of composting	Fungi isolated
0	*Mucor abundans*	8	*Mucor varians*
	M. varians		*Cephalosporium* sp.
	Acrostalagmus albus		*Fusarium* spp.
	Alternaria tenuis		*Penicillium* spp.
	Aspergillus terreus		
	Cephalosporium acremonium		
	Fusarium sp.		
	Gliocladium penicilloides		
	Oospora variabilis		
	Penicillium spp.		
26	*Mucor varians*	26	*Mucor abundans*
	Aspergillus terreus		*Aspergillus* sp.
	Cephalosporium acremonium		*Cephalosporium acremonium*
	Fusarium spp.		*Fusarium* spp.
	Oospora variabilis		*Penicillium* spp.
	Penicillium spp.		

Table 4. *Fungi isolated from straw compost*

Centre of compost		Side of compost (3 in. from edge and 6 in. below surface)	
Days of composting	Fungi isolated	Days of composting	Fungi isolated
0	*Mucor spinescens*	10	*Mucor spinescens*
	Zygorrhynchus moelleri		*Aspergillus fumigatus*
	Aspergillus fumigatus		*Monotospora* sp.
	A. terreus		*Trichoderma viride*
	Monotospora sp.		*Chaetomium globosum*
	Penicillium spp.		
	Trichoderma viride		
	Chaetomium globosum		
	Basidiomycete mycelium		
30	*Aspergillus fumigatus*	20	*Aspergillus fumigatus*
	A. terreus		*A. terreus*
	Monotospora sp.		*Trichoderma viride*
	Penicillium sp.		*Chaetomium globosum*
	Trichoderma viride		Basidiomycete mycelium
	Chaetomium globosum		

The appearance of sporophores of *Coprinus lagopus* was of particular interest in one compost. Chemical analysis of the straw showed a marked fall in cellulose content just before the onset of fruiting by the fungus (Table 6).

In pure culture, *C. lagopus* isolated from a straw compost grows and fruits well on cellulose media (Eastwood, 1949).

DISCUSSION

The quantitative results in this work show that for all composts the fungus flora at the centre of the heap (where the temperature reaches about 65° C.) is destroyed. Survival of fungi is confined to the edges.

After the high-temperature phase there is a very marked development of fungi in the straw composts throughout the material. In the grass some development of surviving fungi around the sides is initiated but conditions, particularly in the centre of the material, appear to be adverse for fungal development, viz. inadequate aeration, alkalinity and very active bacterial growth (Webley, 1947*b*). The straw compost, on the other hand, does not compact but retains an open texture owing to the rigidity of the material, which becomes less alkaline during the composting period.

Table 5. *Microscopic examination of straws*

Organism	Relative frequency*
Perithecia of *Chaetomium globosum*	58
Monotospora sp.	26
Aspergillus sp.	8
Actinomycetes	4
Basidiomycete mycelium	3

* Expressed as a percentage of the total number of recognizable organisms.

Table 6. *Cellulose content of straw during composting*

Days of composting	Cellulose (percentage oven-dried material)	
0	48·8	
10	54·7	
30	57·2	
45	52·2	
52	37·7	Succession of sporophores during this interval
95	36·67	

Qualitative observations indicate some differences in the fungus flora in the two types of compost. These are largely due to the greater development of cellulose decomposers in the straw. Two of the organisms, *Chaetomium globosum* and *Coprinus lagopus*, are now being studied in pure culture from the point of view of the role they play in the decomposition of cellulose and other carbohydrates.

This work was carried out in part with the aid of a grant from the Agricultural Research Council to whom acknowledgement is made. The writer also wishes to thank Dr D. M. Webley for his help and advice during the work.

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BROWN CORE ROOT ROT OF *PRIMULA* CAUSED BY *PHYTOPHTHORA PRIMULAE* N.SP.

By J. A. TOMLINSON

Plant Pathology Laboratory, Harpenden, Herts

(With Plates 8 and 9, and Six Text-figures)

A new disease of polyanthus is shown to be caused by a species of *Phytophthora*, hitherto undescribed. The symptoms and records of the disease are described, as are pathogenicity experiments to polyanthus, related species of *Primula* and other hosts. A detailed description is given of the morphological and cultural characters of the *Phytophthora* which is named *P. primulae*. The mode of infection of the parasite, seasonal characters of the disease and control measures are briefly discussed.

In May 1949, diseased specimens of polyanthus (*Primula polyantha* Mill.) and *Primula* of an unknown species were received at the Ministry of Agriculture and Fisheries' Plant Pathology Laboratory, Harpenden, from Lewes, Sussex. Later the same month polyanthus plants showing the same symptoms were received from Cornwall. All the plants were infected by a species of *Phytophthora*. In May 1950, the same disease was again found in Cornwall as well as in Hertfordshire, Warwickshire and Northumberland, and in 1951 it was seen in Buckinghamshire, Hampshire and Essex. The disease has now been recorded once on primula and ten times on polyanthus.

SYMPTOMS

The symptoms of the disease closely resemble those of the Red Core disease of strawberry (Hickman, 1940). Diseased plants are characteristically dwarfed, and the leaves wilt and collapse in succession from the outside to the centre of the rosette. There is a poorly developed root system with a conspicuous absence of fine lateral roots. Some of the main roots are decayed backwards from the tip, giving a 'rat-tail' effect and affected roots, when cut longitudinally, show a complete discoloration of the vascular tissue as in strawberry Red Core, although the discoloration is brown, hence the proposed disease name Brown Core. Such roots may be entirely without lateral roots. In the development of the disease, however, earlier stages of root infection may be observed. Thus, some roots may be healthy except for partial or general watersoaking and decay of the laterals; while other roots may show both partial loss of laterals and partial discoloration of the stele.

The steles of old infected roots contain large numbers of oospores. When first examined microscopically after teasing in 0·01% cotton-blue dissolved in lactophenol, steles of affected roots were found to contain oospores of two sizes (Pl. 8, fig. 1): the small ones measured 10–26μ, the larger ones 23–33μ in diameter, and they belonged respectively to *Pythium* and *Phytophthora*.

Search through the literature revealed no record of a *Primula* root rot with the symptoms described, but related fungi have been reported on *Primula* spp. on three occasions. Oyler (1937) demonstrated that a strain of *Phytophthora cactorum* (Leb. & Cohn) Schroet. was capable of producing local lesions in stems and petioles of *Primula obconica* Hance; Cook and Collins (1937) recorded the association of *Pythium spinosum* Sawada with a wilt in seedlings of *Primula sinensis* Lindl., and Williams (1947) successfully inoculated petioles of *P. obconica* with a species of *Pythium*.

ISOLATION

Isolations made from roots showing the intermediate stages of infection were most successful in yielding the parasite. They were made in the following manner. Whole roots were severed from the rootstock, washed in running tap water for at least 12 hr. and immersed in 70% alcohol for 10–12 sec. After surface sterilization the roots were washed in several changes of sterile distilled water and cut into lengths 5 mm. long. Using sterile needles the stele of each length was dissected out, placed on plates of maize-extract agar and incubated at laboratory temperatures. After 1–2 days non-septate, finely granular mycelium grew into the agar medium. From the majority of steles a fast-growing species of *Pythium* was obtained which formed abundant oospores closely resembling the small oospores found earlier in diseased polyanthus vascular tissue. The *Pythium* was isolated constantly and it overgrew all other isolates, including a second oomycete (obtained from 5% of the steles) which produced a stiffly branched mycelium characteristic of *Phytophthora*. Its growth was slow compared with that of the *Pythium*, and only rarely made sufficient headway for subcultures to be prepared. Three days after subculturing, oogonia with paragynous antheridia and oospores began to form, at first sparingly and then abundantly. They closely resembled the larger oospores found earlier in diseased vascular tissue.

Species of *Penicillium*, *Mucor* and *Fusarium* were occasionally isolated and on one occasion another *Pythium*, thought to be *P. oligandrum* Drechsler, was obtained, but none of these was regarded as the cause of the disease and no further experiments were done with them. The species of *Pythium* constantly isolated was identified as *P. aphanidermatum* (Edson) Fitzpatrick, and was indistinguishable from an authentic culture of this fungus kindly supplied by Dr C. J. Hickman: the species of *Phytophthora* could not then be identified. Isolates of both fungi were freed from bacterial contamination using Raper's technique (1937), and stock cultures were established on bean-meal agar.*

PATHOGENICITY EXPERIMENTS

Inoculation of Primula

Proof of pathogenicity towards polyanthus was obtained in the following manner. Polyanthus plants were grown in a John Innes potting compost and when well established were divided into four sets of equal number.

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* Ground seeds of dwarf bean (variety Canadian Wonder) 50 g., agar 20 g., water 1000 c.c. Bean powder stirred into the water and boiled for 5 min.; agar added, dissolved and medium tubed.

Two sets were inoculated with the isolate of *Pythium aphanidermatum*, one set receiving agar disks of young mycelium, the other a suspension of zoospores. The other two sets were treated in the same manner but with the *Phytophthora* isolate. Plants inoculated with sterile agar disks and sterile distilled water served as controls. Disks of agar inoculum were cut from the edge of an actively growing bean-meal agar colony using a 1 cm. cork-borer. Four disks were inserted near the crown of the plant to a depth of ½ in. Plants watered with zoospores each received 50 c.c. from a stock zoospore suspension obtained by a method described below.

The first visible result of the inoculations was observed after 5–6 weeks when the plants inoculated with *Phytophthora* were seen to be smaller than those in the *Pythium aphanidermatum* and control sets. This dwarfing subsequently became more pronounced, the affected plants making negligible growth. After 10 weeks the outer leaves of the majority of dwarfed plants collapsed and died, and this was followed by wilting of the inner leaves within a period of 5 days (Pl. 8, fig. 2). When washed and examined these plants showed a greatly reduced root system and an almost complete loss of lateral roots, and the steles of the main roots were discoloured brown (Pl. 9). Microscopical examination showed that the vascular tissues contained a large number of oospores similar in size to those found in the original roots and produced by the *Phytophthora* in pure culture. The *Phytophthora* was successfully re-isolated six out of eight times. The control plants and those inoculated with *Pythium aphanidermatum* remained healthy and flowered after 10 weeks' growth. The experiment was repeated twice with identical results.

Further experiments to test the pathogenicity of the *Pythium* and *Phytophthora* to other species of *Primula* were made by inserting small pieces of young bean-meal agar cultures into small wounds made in the roots of *Primula denticulata* Sm. and *P. wanda* Hort. An incision was made through the cortex to the stele, using a sterile scalpel. After inserting the inoculum the wound was covered with absorbent cotton-wool and bound with 'Stericrepe'. One half of the roots of twelve plants of each species were inoculated, and six plants identically treated except for the omission of inoculum served as controls. After inoculation the plants were potted up and placed in a cold greenhouse. When examined 6 weeks later they were all healthy. The experiment was repeated using *P. denticulata* and the same result was obtained. In a third experiment both species of *Primula* were grown in compost with which cultures of the two isolates from polyanthus had been thoroughly mixed, and again no infection resulted. As Brown Core symptoms have been produced in polyanthus plants by mixing cultures of the polyanthus *Phytophthora* with potting compost it would appear that *P. denticulata* and *P. wanda* are both resistant to the disease.

Cowslip (*Primula veris* L.) and primrose (*P. vulgaris* Huds.) were inoculated with the polyanthus *Phytophthora*, some with a zoospore suspension and others by means of four disks of bean-meal agar cultures. The primrose plants developed typical Brown Core symptoms, but the cowslips remained healthy.

Inoculation of other plants

Various plants were inoculated in order to study the host range of the polyanthus *Phytophthora*. They were: apple fruits (Beauty of Bath, Duchess of Oldenburgh, Lady Sudeley, Red Astrakhan, Worcester Pearmain); potato (Arran Banner, Majestic); onion (Ailsa Craig, Spanish White); tomato (Early Market, Harbinger); strawberry (Huxley), and wild strawberry (*Fragaria vesca* L.). The fungus was successfully re-isolated from all diseased specimens.

Apple fruits were wound inoculated by inserting with a sterile scalpel a small piece from an actively growing bean-meal agar culture of the fungus beneath a small flap of tissue cut in the side of the fruit. Controls were treated identically except for the insertion of the inoculum. Potato tubers were inoculated at the heel-end, and onion bulbs in the centre of the basal plate. The fruits, tubers and bulbs were placed on moistened filter-paper inside large glass dishes fitted with lids, and kept at room temperature. Young tomato plants 6–8 in. high were inoculated in the stem about 3 in. above the soil surface, agar inoculum of the fungus being inserted into a slit made in the stem after previous surface sterilization. The wound was bound with absorbent cotton-wool kept in position with stericrepe. The cotton-wool was saturated with sterile distilled water at intervals and the experiment run under greenhouse conditions with an average daily temperature of 75° F. Strawberry plants were inoculated with zoospores and agar disks in the manner described for polyanthus.

Pathogenicity to the five varieties of apple was demonstrated as a brown, circular rot spreading from the wound (2·5 cm. in diameter after 10 days at laboratory temperature). All plants of both varieties of tomato inoculated developed a dark lesion on the stem around the site of inoculation, and the part of the plant above it collapsed and died. Uninoculated apple fruits and tomato plants remained healthy. The fungus was non-pathogenic to potato tubers, onion bulbs, and cultivated and wild strawberries. Attempts to produce Brown Core symptoms in polyanthus roots with *Phytophthora fragariae* also gave negative results.

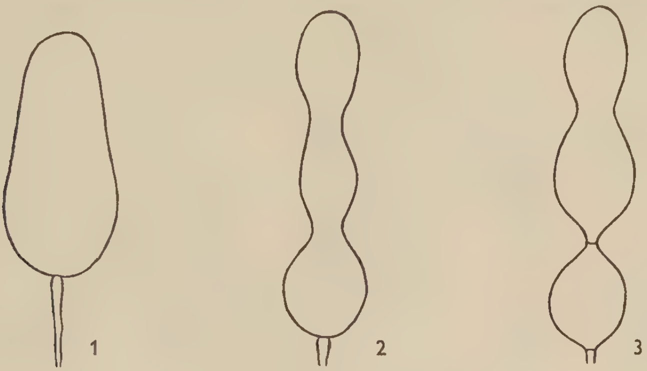
CHARACTERS AND IDENTIFICATION OF THE POLYANTHUS *PHYTOPHTHORA*

Morphology

The following description is based on an isolate from the type material from Sussex, for little cultural or morphological variation between isolates from Cornwall, Sussex and Northumberland has been observed.

The vegetative growth of the fungus is typical of the genus *Phytophthora*. Individual hyphae show the characteristic right-angled branching with a slight constriction at the base of each branch (Blackwell, 1949). The hyphae are commonly 4–6 μ in diameter. Compared with *P. cryptogea* Pethybr. & Laff. and *P. parasitica* Dast., the development of aerial mycelium on oat- and bean-meal agars is slight. In the development of coiled hyphae on some media, the fungus recalls the habit of *P. porri* (Foister, 1931). In old cultures the mycelium becomes devoid of protoplasm and septa are frequent. Sporangia form sparingly when pieces of old infected root are immersed in aerated soil-extract solutions but they develop in greater numbers from young infected roots, and particularly from infected lateral roots. The development, form and germination of sporangia were carefully studied at laboratory temperatures (15–20° C.) from bean-meal agar disks placed in sterile, filtered soil-extract solution* through which was passed a continuous stream of air bubbles. These conditions, of those tried, proved the optimum for asexual reproduction, sporangia and zoospores forming in great numbers.

Sporangia are borne terminally on undifferentiated sporangiophores 10–500 μ long, which may occasionally show one or more subsporangial swellings. The sporangia vary greatly in shape and size and a developmental series can be traced, the essential features of which are illustrated in Text-fig. 1. In addition to sporangia typical of *Phytophthora* (1), the fungus produces forms with a tendency towards constriction (2) and also forms in which the constricted portions become separated from each other by septa to form distinct segments (3). Whereas the protoplasmic contents as a whole of forms (1) and (2) germinate by zoospores, only the terminal segment of form (3) may do likewise.



Text-fig. 1.

Camera lucida drawings of these three stages are shown in Text-figs. 2–4.

The simple forms of sporangium may be ovoid, bluntly ellipsoid, limoniform or slightly more irregular or constricted (Text-fig. 2). They measure 33–165 × 23–52 μ (average 77 × 34 μ). Text-fig. 3 *D–F*, illustrate forms of sporangium with pronounced constrictions at one or more places along the length of the sporangium.

Text-figs. 3 *B* and 4, illustrate some of the more commonly found forms of sporangium in which segmentation follows constriction. I believe these forms represent a development hitherto undescribed in the genus *Phytophthora*. Thus, the sporangium illustrated in Text-fig. 3 *B*, when first formed, consisted of three segments (1–3) following the formation of septa at two constrictions (S_1 and S_2) and delimitation of the sporangiophore (S_3). The terminal segment (1) then produced a germ tube (*g*) and gave rise to an identical segment (4) above it into which passed its

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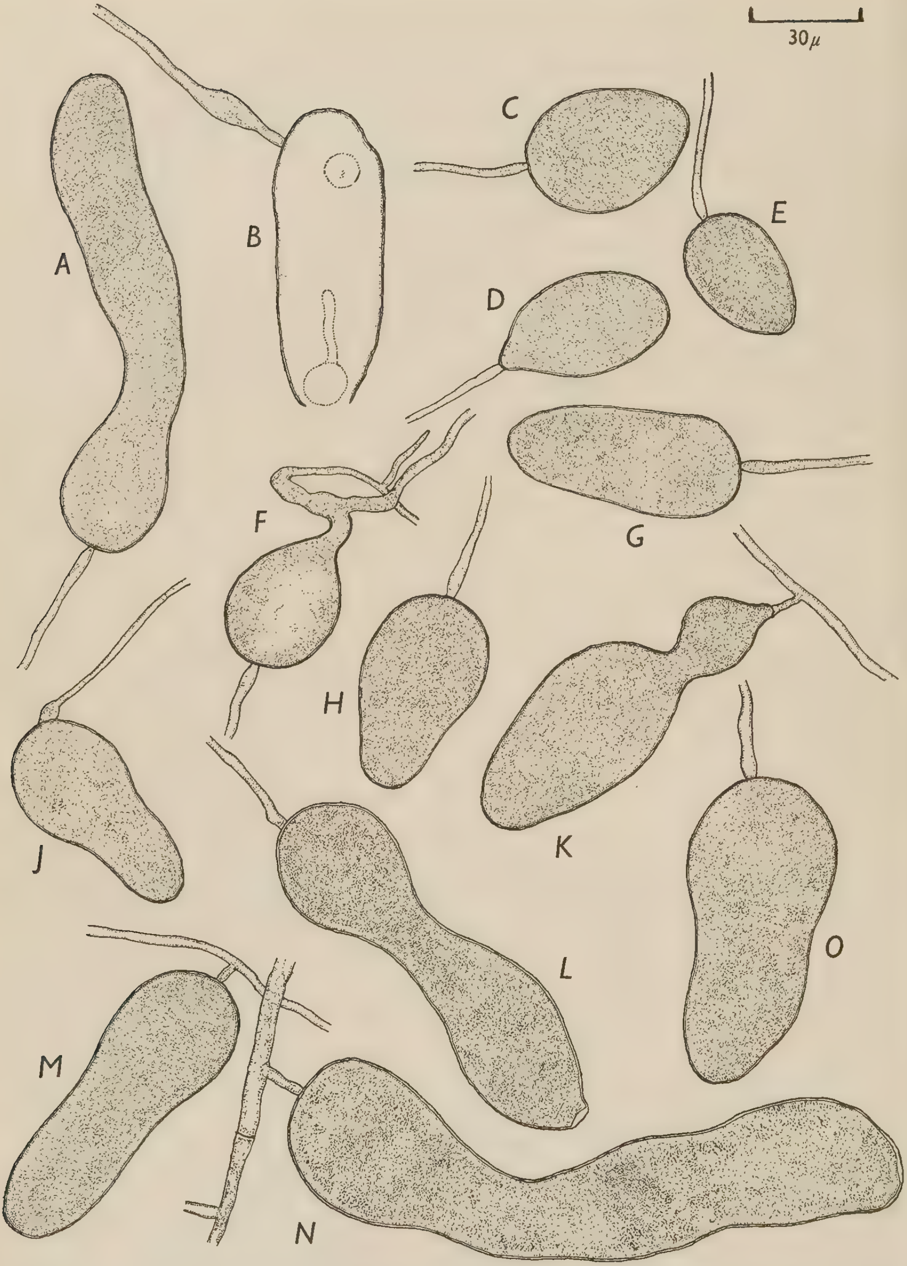
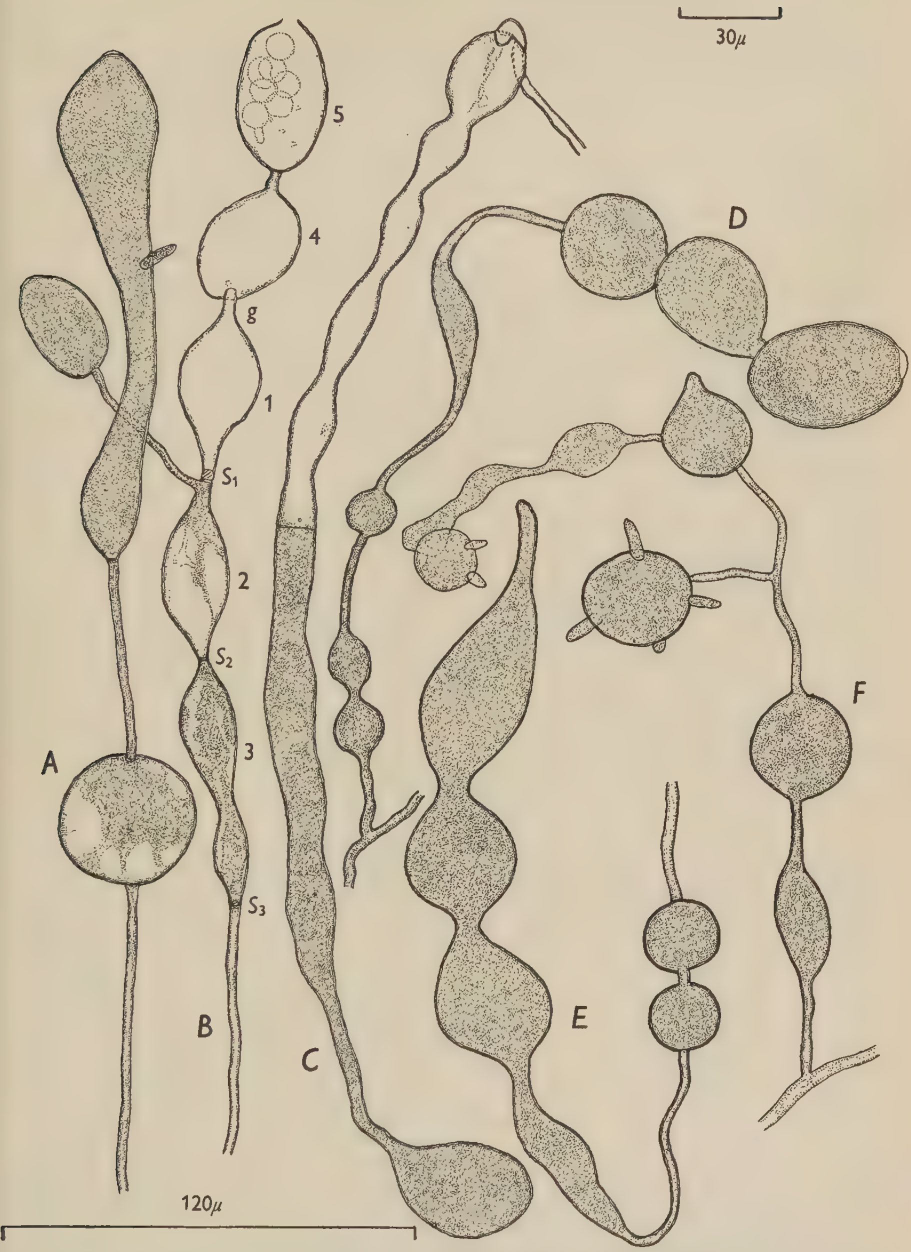
* Soil 100 g., distilled water 200 c.c. The suspension is shaken and filtered, and the filtrate is further cleared by centrifuging.

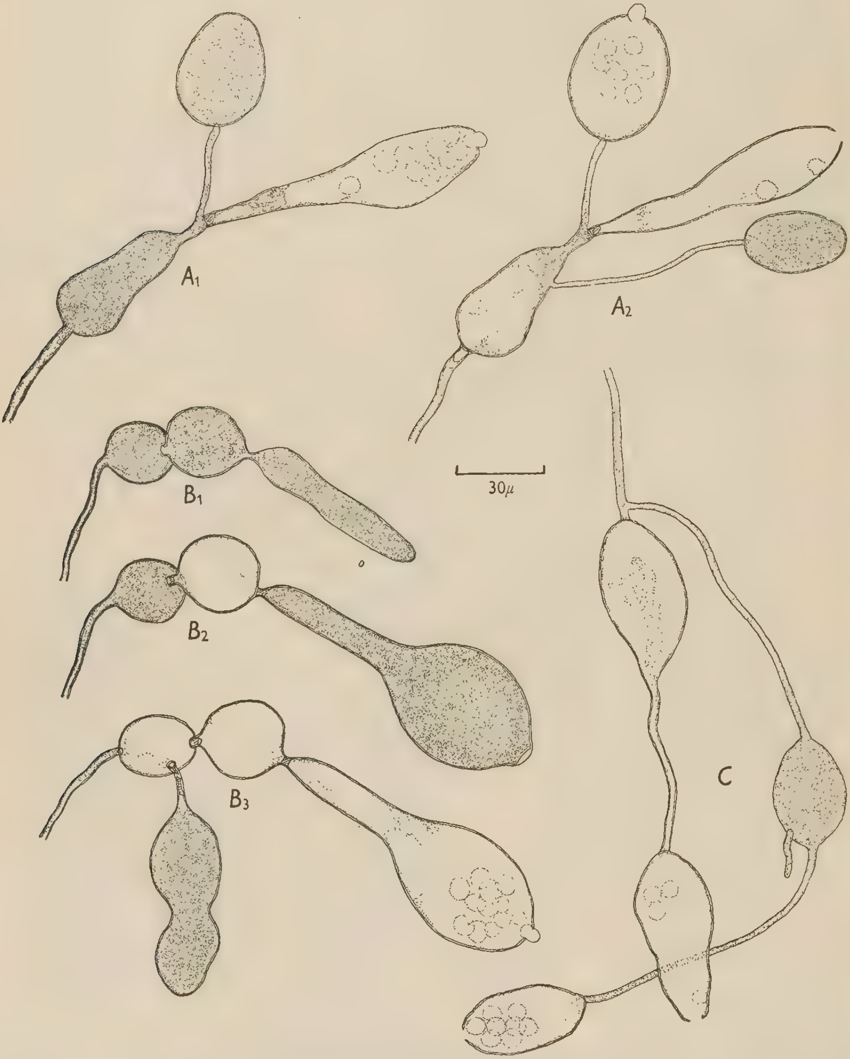


Text-fig. 2. *A–O*, sporangia of *Phytophthora primulae* produced from culture-disks of bean-meal agar immersed in aerated, soil-extract solution after 3 days. *A*, *N*, *K* and *L*, sporangia with slight constrictions occurring along the length of the sporangium; *B*, an excentrically-borne sporangium having germinated by zoospores. One of the two unescaped zoospores has germinated and produced a short germ tube; *F*, an ovoid sporangium germinating directly.



Text-fig. 3. *A–F*, sporangia of *Phytophthora primulae* produced from culture-disks of bean-meal agar immersed in aerated, soil-extract solution after 3 days. *A*, direct germination of an elongated form of sporangium borne terminally on a long sporangiophore with a large, spherical, subsporangial swelling; *C*, an elongated form of sporangium in which the protoplasmic contents occupied the terminal half of the sporangium only and (later) gave rise to zoospores; *B* and *D–F*, compound sporangia with pronounced constrictions occurring along the length of the sporangium.

protoplasmic contents. This terminal development was repeated so that the last two subterminal segments (1 and 4) became empty as illustrated. Zoospore germination of the terminal segment (5) then followed. The



Text-fig. 4. *A–C*, sporangia of *Phytophthora primulae* produced from culture-disks of bean-meal agar immersed in aerated, soil-extract solution after 3 days. A_1, A_2, B_1, B_2 and B_3, progress of the development of two compound sporangia drawn by camera lucida at intervals of 3 hr.; *C*, direct germination of a sporangium and of a sympodially produced secondary sporangium. In both instances the sporangium finally produced germinated by zoospores.

remaining ungerminated segments of the chain disintegrated in the one instance (3), and produced a secondary sporangium (2) in the other.

The same basic steps occurred in the development of the sporangium illustrated in Text-fig. 4, B_1, B_2 and B_3. Here the development is traced at intervals of 3 hr. and shows the fate of each segment; that nearest the sporangiophore germinating to produce a secondary sporangium, the middle segment contributing its contents to the development of a terminal segment, and the latter germinating by zoospores.

In Text-fig. 4, A_1, A_2, a third segmented form is illustrated in which no terminal development occurs. The initially formed terminal segment germinated by zoospores, while the subterminal segment, due to its late separation from the sporangiophore and early, direct germination, itself produced two secondary sporangia.

I propose to call these segmented bodies compound sporangia. They have been repeatedly produced in the first flush of growth under good conditions and in no way represent irregularities that may occur in other species of *Phytophthora* when grown under unfavourable conditions. They measure $100\text{–}351 \times 6\text{–}36\,\mu$.

The sporangia are either non-papillate, or have a shallow inconspicuous papillum. Germination usually occurs by the liberation of zoospores formed *in situ*, after the disappearance of the slightly thickened apical part of the wall. Direct germination by the formation of one or more germ tubes also occurs at the apex or just behind the apex of the sporangium. Zoospores were examined microscopically using a $\frac{1}{8}$ in. objective after adding a trace of potassium iodide solution to 1–2 drops of zoospore suspension. In this way their movements were decelerated sufficiently to make their biflagellate nature faintly visible. Zoospores that encysted were spherical and from $10\text{–}15\,\mu$ in diameter, germinating by germ tubes. Single zoospore cultures produced mycelia with reproductive organs of both kinds, thus demonstrating homothallism.

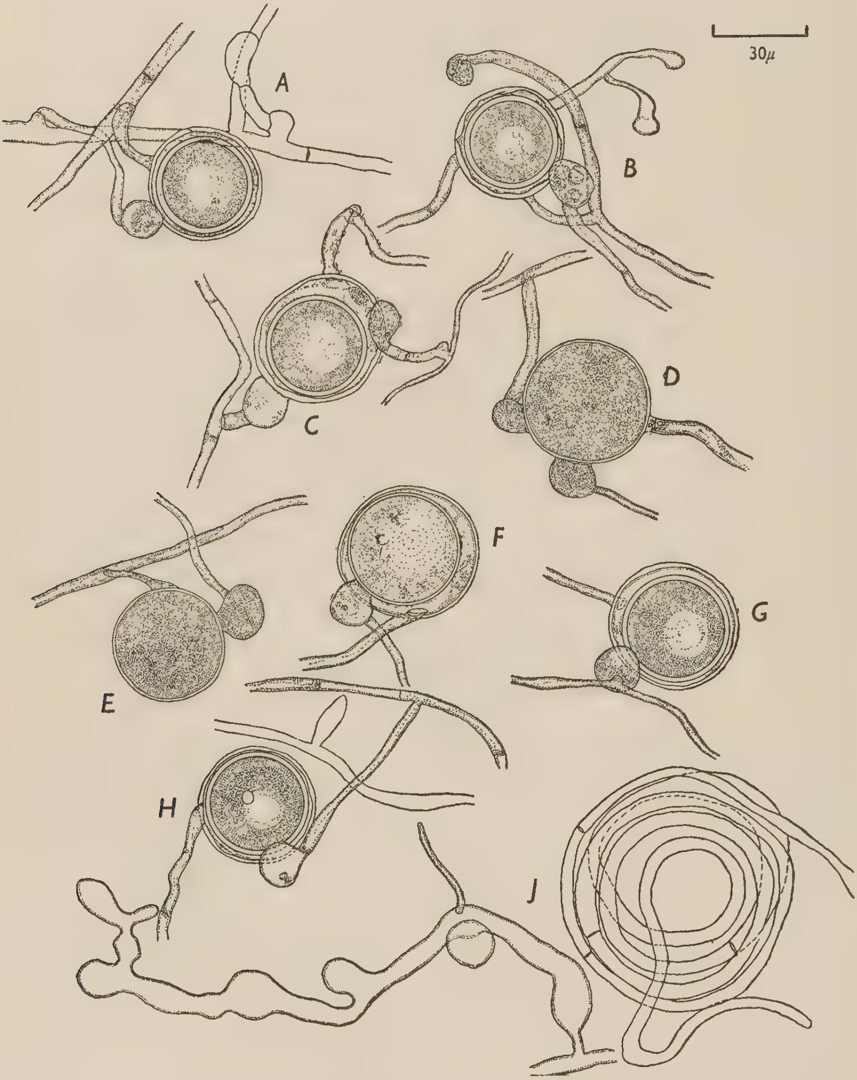
The production of secondary sporangia very occasionally occurs with the formation of a monochasial sympodium but proliferation has not been observed.

Sexual organs (Text-fig. 5) are formed readily and abundantly in diseased vascular root tissues and on agar media. Oogonia are terminal or lateral, smooth, hyaline and vary from 23 to $43\,\mu$ (average $37\,\mu$) in diameter. The oogonium encloses an oosphere which, after fertilization, develops into a spherical oospore occupying most of the interior of the oogonium, and lying freely within it. At maturity the oospore varies from 17 to $33\,\mu$ (average $30\,\mu$) in diameter. It contains finely granular protoplasm, a single large excentric oil globule and a large central vacuole. The oospore wall is smooth, hyaline and $3\,\mu$ in thickness. Antheridia are always paragynous and are formed as terminal cells of lateral branches. Oogonia with two antheridia have been found but only one antheridium takes part in fertilization.

Growth in pure culture

The fungus was grown on a variety of media to obtain data on mycelial growth and the type and abundance of reproductive organs. The media used were bean-meal agar (bean meal 50 g., agar powder 20 g., distilled water 1000 c.c.); oat-meal agar (oat meal 25 g., agar powder 20 g., distilled water 1000 c.c.); maize-extract agar (maize meal 50 g., agar powder 20 g., distilled water 1000 c.c.); malt agar (dry malt extract

5·0 g., potassium dihydrogen phosphate 0·6 g., magnesium sulphate 0·3 g., agar powder 20 g., distilled water 1000 c.c.) and potato-dextrose agar (potato tuber 200 g., dextrose 20 g., agar powder 20 g., distilled water 1000 c.c.).



Text-fig. 5. *A–H*, sexual organs of *Phytophthora primulae* in 3-week-old bean-meal agar cultures. *A–C* and *F*, *H*, oogonia, oospores and terminal, diclinous, paragynous antheridia; *D*, oogonium with two antheridia prior to fertilization; *G*, oogonium, oospore and an intercalary, diclinous, paragynous antheridium; *J*, a hyphal coil and a terminal hyphal swelling occasionally found in agar culture.

At ordinary laboratory temperatures (15–20° C.) on most media, a slowly growing, highly branched mycelium develops, approximately 5 cm. in diameter after 7 days. The degree of branching and production of aerial mycelium varies with the type of agar, being greatest on potato-dextrose and least on malt agars. In 3–4-week-old oat-meal agar cultures sporangia were occasionally found on the surface of the medium, or projecting above it on short sporangiophores. In tube cultures of bean-meal agar sporangia occasionally formed in drops of water entangled in the aerial mycelium. Sporangia were rarely found on malt agar and were absent on maize-extract and potato-dextrose agars. Sexual organs were absent on malt agar. They formed abundantly and readily (5 days) on bean-meal and oat-meal agars, and frequently on maize-extract (5 days) and potato-dextrose (10 days) agars.

The growth-temperature relations of the polyanthus *Phytophthora* were determined on plates of maize-extract agar. Its linear spread was compared with the polyanthus isolate of *Pythium aphanidermatum*. Precautions were taken to standardize the depth of medium in Petri dishes to 4 mm. and the quantity and age of inoculum was standardized by taking 3 mm. squares of agar from the advancing edge of a circular colony. Daily measurements of two diameters at right angles to each other were recorded to the nearest millimetre from the more or less circular growth which resulted. The range of temperatures used was: -4, 2, 10, 17, 24, 27, 30, 35, 40 and 45° C. The growth rates of the fungus after 10 days and of *P. aphanidermatum* after 2 days are shown in Text-fig. 6.

The optimum, minimum and maximum growth temperatures of the polyanthus fungus were respectively 15–20° C., slightly above freezing-point, and slightly below 27° C. By comparison with other species of *Phytophthora* and with *Pythium aphanidermatum*, the fungus would appear to be a slow-growing organism with a preference for low temperatures. It is a third species of *Phytophthora* with a thermal death-point of 27° C., the other two being *P. hibernalis* Carne and *P. syringae* (Kleb.) Kleb. (Leonian, 1934).

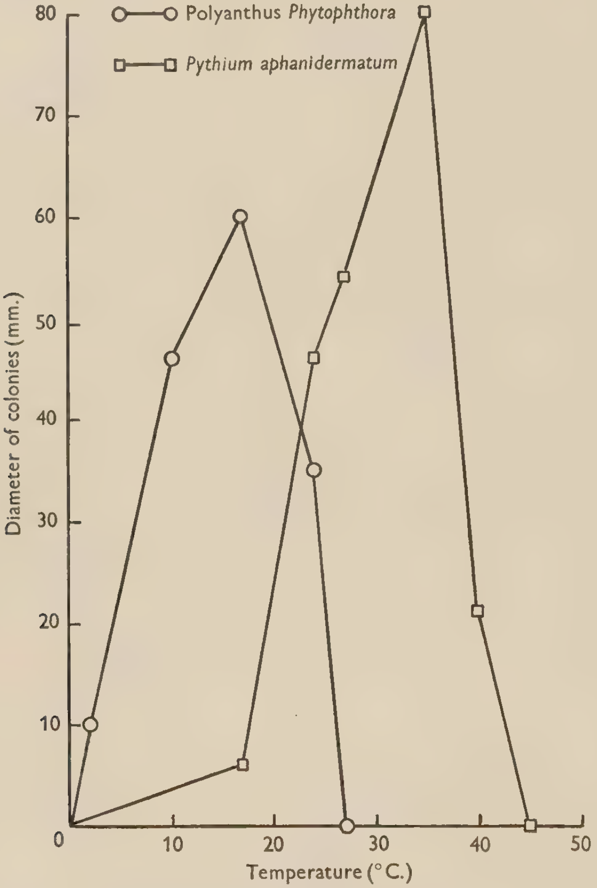
Some morphological differences were noted. At 17° C. the fungus produces smooth hyphae, and abundant sexual organs, whereas at 24° C. hyphal swellings occur and sexual organs are absent.

Identity

Using Tucker's (1931) key, the polyanthus *Phytophthora* could be identified as *P. syringae* (Kleb.) Kleb. on account of its growth on malt agar at 20° C., predominantly paragynous antheridia on oat-meal agar at 20° C. and failure to grow at 27° C. There are certain features, however, which made this identification unacceptable.

In describing *P. syringae* Klebahn (1909) states: 'Sporangien eiförmig, verkehrt eiförmig oder ellipsoidisch, 40–75: 30–42 μ, nur im Wasser entstehend, einzeln endständig an dünnen Fäden oder zu mehreren (bis 7) in sympodial entwickelten Sporangienständen vereinigt, am Ende mit einem flachen Deckel, der bei der Entleerung verquillt und eine weite, abgestutzte Öffnung zurücklässt.' The sporangia of the polyanthus fungus are thus much larger than those of *P. syringae*. Further, there is no mention in the literature of sporangial features resembling the compound sporangia of the polyanthus *Phytophthora*. Finally, the occurrence of amphigynous antheridia discovered in *P. syringae* by Lafferty and Pethybridge (1922) also serves as a distinguishing feature.

Comparison was also made with sixteen species of *Phytophthora* erected between 1931 and 1949. They are: *P. megasperma* Drechsler (1931), *P. porri* Foister (1931), *P. cinchonae* Sawada (1936), *P. stellata* Shanor (1938), *P. fragariae* Hickman (1940), *P. verrucosa* Alcock & Foister (Foister, 1940), *P. macrospora* (Sacc.) Ito & Tanaka (Tanaka, 1940), *P. leesiae* Sawada (1941), *P. lateralis* Tucker & Milbrath (1942), *P. formosana* Sawada (1942*a*), *P. lycopersici* Sawada (1942*b*), *P. ricini* Sawada (1942*c*), *P. murrayae* Sawada (1942*d*), *P. quininea* Crandall (1947), *P. himalayensis* Dastur (1948) and *P. inflata* Caroselli & Tucker (1949).



Text-fig. 6. Influence of temperature upon the growth of *Phytophthora primulae* and *Pythium aphanidermatum*.

Of these species *P. megasperma*, *P. macrospora* and *P. quininea* are readily distinguishable from the polyanthus fungus in the possession of much larger sexual organs, while *P. leesiae*, *P. formosana*, *P. lycopersici*, *P. ricini* and *P. himalayensis* have amphigynous antheridia. Oospores of *P. murrayae* are unknown, and its sporangia in no way resemble the compound sporangia of the polyanthus *Phytophthora*. *P. verrucosa* with verrucose oogonial walls, *P. stellata* with stellate oogonial walls, *P. inflata* with inflated, usually variously contorted and twisting antheridia and *P. lateralis* with its abundant chlamydospores and very small sporangia are also clearly different. *P. fragariae* and *P. cinchonae* have smaller sporangia and give rise to secondary sporangia by proliferation, and *P. porri* has both amphigynous and paragynous antheridia and produces secondary sporangia regularly by sympodial branching.

Thus the polyanthus *Phytophthora* cannot be identified with any previously described species, and I therefore propose to name it:

Phytophthora primulae sp.nov.

Hyphae hyalinae, primo continuae, demum septatae et vetustate protoplasmate vacuae, aliquando spiraliter torsae. Sporangiophora non a mycelio distincta, 10–500 μ longa. Sporangia terminalia, in forma et magnitudine variabilia; alia simplicia, ovoidea, obtuse ellipsoidea limoniformia vel obpyriformia, 33–165 × 23–52 μ (med. 77 × 34 μ); alia elongata, multiplicia, e 2–11 partibus spaericia vel irregularibus a septis vel obturaculis hyalinis divisis et catenatim conjunctis composita; vulgo non papillata vel papilla pertenue praedita, per zoosporas vel tubum germinantia. Sporangia secundaria aliquando nascentia, ita ut sympodium monochasiale productum est. Zoosporae 10–15 μ diam. Antheridia et oogonia semper copiosa, et in textu radicis et in agare culta. Oogonia terminalia vel lateralia, globosa, 23–43 μ (med. 37 μ) diam. Antheridia terminalia, rarius intercalaria, diclina et paragyna, saepissime 14–18 μ diam. Oosporae sphaericae, primo hyalinae, interdum vetustate lutescentes, 17–33 μ (med. 30 μ) diam. episporio laevi, 3 μ crasso. Hab. in radicibus *Primulae polyanthae* Mill., parasitica.

Mycelium hyaline, non-septate when young, septate and devoid of protoplasm when old; occasionally coiled in spirals. Sporangia terminal, developed on undifferentiated sporangiophores 10–500 μ long; in shape and size exhibiting great variation; some, single structures, ovoid, bluntly ellipsoid, limoniform or obpyriform, 33–165 × 23–52 μ (average 77 × 34 μ); others compound forms (compound sporangia), elongated structures consisting of two to eleven spherical or more irregularly shaped sporangial segments delimited at one or both ends by septa or hyaline plugs and connected in chain fashion, 100–351 × 6–36 μ; generally non-papillate or with a shallow inconspicuous papillum germinating by zoospores or germ tubes. Zoospores 10–15 μ. Sporangia formed very occasionally with the development of a monochasial sympodium. Sexual organs formed abundantly in vascular tissue and in artificial culture. Oogonia terminal or lateral, globose, 23–43 μ (average 37 μ) in diameter. Antheridia terminal, rarely intercalary, diclinous and paragynous, mostly 14–18 μ in diameter. Oospores spherical, hyaline when young, sometimes light yellow when old, 17–33 μ (average 30 μ) in diameter, with a smooth wall 3 μ in thickness.

Habitat. In the roots of *Primula polyantha* Mill. causing a stele discoloration and root rot in England (Herbarium Plant Pathology Laboratory, Harpenden, Herts, No. 965, Type).

Discussion

Though the symptoms of *Primula* Brown Core and strawberry Red Core are strikingly similar, experiments have shown that in morphology and pathogenicity the two organisms responsible for these diseases are distinct. Special attention is drawn to two similarities between the two diseases. In preliminary experiments on the mode of infection of the *Primula* parasite, whole root systems of polyanthus plants were dipped in a zoospore suspension of the *Phytophthora* for 24 hr. After treatment the plants were potted in sterilized, fine, sandy loam watered with sterile distilled water and examined at daily intervals for 3 weeks by removing the inoculated plants and carefully washing the roots. Observations showed that the fine lateral roots became affected first, brown discoloured steles being detected in them after 2–3 weeks, first near the tip of the root and spreading backwards towards the main root. It therefore seems unlikely that the fungus gains entry into the steles of main roots via the cortical tissues, but reaches them only after infection and growth through the lateral roots. Hickman (1940) also was unable to trace direct infection of the main roots of strawberry by *P. fragariae*. It is hoped to carry out more detailed work on the mode of entry of zoospores of *P. primulae* into *Primula* roots.

The late spring wilting and collapse of diseased *Primula* plants is another character which this disease has in common with strawberry Red Core, for of the eleven records of Brown Core so far made, three were reported in late April and eight in May. As with Red Core, diseased polyanthus plants cease to grow, remain conspicuously dwarfed and ultimately wilt.

Polyanthus is cultivated commercially out-of-doors mainly in the southern counties, and for the cut-flower trade. In one nursery of this kind which I visited, the disease had affected several thousand plants and was rapidly becoming a menace. Attacks on the field were found to have originated in the seedling boxes, the fungus probably being carried over during planting operations in soil adhering to the roots or in roots of slightly affected young plants.

There has been little opportunity so far for experimental work on the control of Brown Core, but in preliminary experiments with soil fungicides tetramethylthiuram disulphide has shown some promise. By taking a few practical precautions, however, the risks of contaminating clean soil and of spreading the disease through the sale of infected plants may be reduced appreciably. Compost for raising seedlings should be made from clean soil, and in nurseries where the disease occurs, steam sterilization of the soil should if possible be practised. As plants may become infected at any stage of growth, seedlings should not be planted in soil where the disease has occurred, for it is probable that the fungus can remain viable in the soil for several years.

I wish to thank Dr C. J. Hickman for pertinent criticisms of earlier drafts of this work, Miss E. M. Wakefield for the Latin diagnosis and Mr W. F. Buck for the photography.

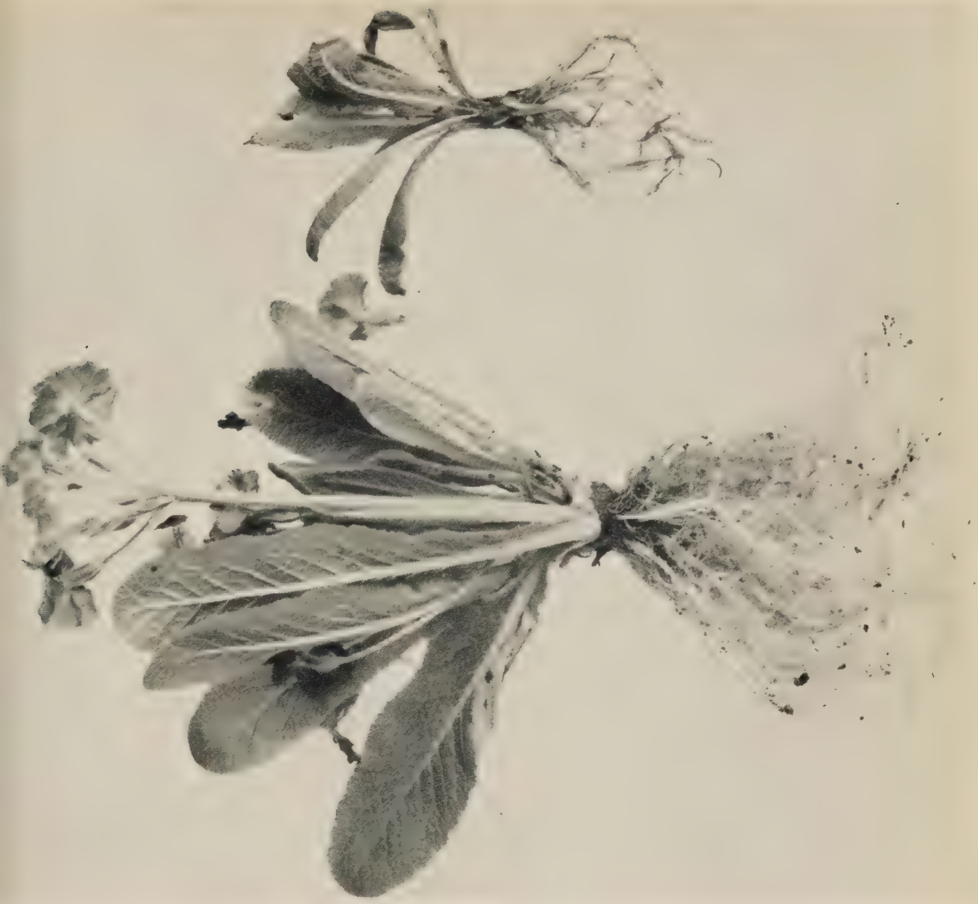


Fig. 2.

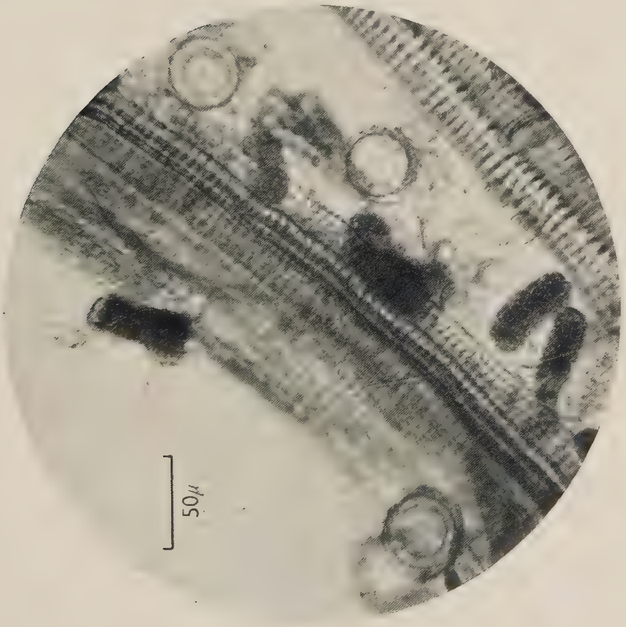


Fig. 1.

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EXPLANATION OF PLATES 8 AND 9

Plate 8

Fig. 1. Photomicrograph of a diseased polyanthus root stele, teased and mounted in 0·01% cotton-blue in lactophenol showing oogonia with oospores of two sizes; the larger ones *Phytophthora primulae*, the smaller ones *Pythium aphanidermatum*.

Fig. 2. Healthy and diseased polyanthus plants 10 weeks after inoculation with *Phytophthora primulae*. On the left a healthy control plant with extensive root system; on the right a diseased plant showing reduced root system and wilted leaves.

Plate 9

The root system of a diseased polyanthus plant 10 weeks after inoculation with *Phytophthora primulae*. The roots have been split longitudinally to show the discoloured steles.

(*Accepted for publication* 3 *December* 1951)

THE NAME *OIDIUM*

By G. R. BISBY

Commonwealth Mycological Institute, Kew

Oidium is a common name in French, English, Italian (as 'oidio') and is sometimes used in other languages. The name is applied to the mildew of the vine or of other plants, or to the conidial states of the Erysiphaceae.

The generic name *Oidium* Link ex Fr. (1832) included different sorts of fungi, three of the eight species being conidial Erysiphaceae. However, Fries designated as type of the genus *Mucor leprosus* L. (= *O. aureum* Link ex Fr.).

Saccardo (1880) proposed *Oidium* 'Link p.p.', gave a Latin diagnosis, and cited 'Exempl. *O. erysiphoides* Fr., *O. Tuckeri* Berk.'. The new Article 47 *bis* of the Rules makes possible the conservation of *Oidium* Sacc., and *O. tuckeri*, the conidial state of the mildew of the vine, would make a good lectotype. I herewith propose that *Oidium* Sacc. be conserved and that *Oidium* Link ex Fr. be rejected.

Those who criticize Saccardo should remember that there were no Rules of Nomenclature for Fungi in 1880. He was ably seeking order amongst the names of fungi, and an important criterion was the usage of that time. By 1880, *Oidium* was commonly used for conidial states of mildew fungi. For more than seventy years the name has been used in Saccardo's sense and there is a vast literature, particularly in plant pathology. No name other than *Oidium* is in use for those species, especially in the tropics, with perfect states unknown.

Linder (1942) monographed *Oidium* Link ex Fr. for fungi congeneric with the type species, *O. aureum*. He noted that *Acladium* Link (1809) has page precedence over *Oidium* Link (1809) but that *Acladium* could not be used because Fries had made it a synonym of *Sporotrichum*. Linder remarked that plant pathologists can use *Acrosporium* Nees (1817) for conidial Erysiphaceae, overlooking the fact that Fries had made that name a synonym of *Oidium*.

Dr D. P. Rogers points out (*in litt.*) that, according to the present Rules, *Acladium* can be cited as Link ex Pers., *Mycol. Eur.* **1**, p. 28, 1822 with *A. conspersum* Link ex Pers. as the first of three species and that the other two were excluded from the genus by Link in 1824. Linder (1942) accepted *A. conspersum* as a good species and noted that Melin and Nannfeldt had examined an authentic specimen sent to Fries by Link. (I do not know that anyone has seen an authentic specimen of *Mucor leprosus* L., the type of the genus *Oidium* Link ex Fr.) *Acladium* (1822) not only antedates *Oidium* Link ex Fr., but seems to provide a sound and unambiguous name for these fungi, many of which have been erroneously placed in *Rhinotrichum*.

As for *Acrosporium*, Rogers writes that it can be cited Nees ex S. F. Gray, *Nat. Arr.*, 1821, with the monotype *A. monilioides* Nees ex Gray. However, *Acrosporium* has not been used except by Sumstine (1913) for a few species.

There is also the genus *Acrosporium* Bon. (1851). It seems very undesirable to try to have *Acrosporium* adopted in place of *Oidium* for conidial Erysiphaceae.

Boedijn (1951) considers that it 'seems not recommendable' to displace *Oidium* for conidial states of mildews. Plant pathologists will agree. If this proposal for the conservation of *Oidium* Sacc. is provisionally approved by the Executive Committee, the name can legitimately be used unless and until the proposal be rejected by a Botanical Congress. If it becomes advisable to coin a new name for conidial Erysiphaceae, it should be a name closely resembling *Oidium*, such as *Odium*.

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(*Accepted for publication* 30 *April* 1952)

MASONIELLA Nom.Nov.

By GEORGE SMITH

London School of Hygiene and Tropical Medicine

Since the publication of '*Masonia*, a new genus of Hyphomycetes', *Trans. Brit. mycol. Soc.* **35**, 139–151, 1952, my attention has been drawn to the fact that *Masonia* Smith (1952), is a later homonym of *Masonia* Hansford (1944), a genus of Ascomycetes. I therefore propose the name *Masoniella* Smith nom.nov. for the hyphomycete genus *Masonia* Smith (1952) non Hansford (1944), with the two species *Masoniella grisea* (Smith) Smith n.comb. (= *Masonia grisea* Smith, 1952), typus; and *Masoniella chartarum* (Smith) Smith n.comb. (= *Masonia chartarum* Smith, 1952).

The type specimens of *Masonia grisea* Smith and *M. chartarum* Smith in Herb. Roy. Bot. Gardens, Kew, and co-types in Herb. I.M.I., Kew, are now filed under the new name *Masoniella*.

(*Accepted for publication* 12 *July* 1952)

REVIEWS

KLIC kurčování našich hub hřibovitých a belovitých (*Agaricalium Europaeorum Clavis Dichotomica*). By Albert Pilát. (Prague, 1951.) Czech Krone, unbound 758, bound 832.

This handsome volume of 720 large pages is written entirely in Czech. We regret that such an important work describing all the known European species of Agarics and Boleti will be intelligible to few outside Czechoslovakia. Even so we shall often have occasion to refer to it. The classification is modern without being revolutionary. Dr Pilát often gives priority to specific names which have not hitherto been adopted. Adequate descriptions are given and the appropriate literature extensively cited. There are no coloured plates but 274 pages are filled with uncoloured photographs, several on each page. The price is high and at the present exchange works out at about £5 unbound and £5. 11*s*. 0*d*. bound in cloth—and well worth the money if only we could read Czech! It is an interesting example of state support to a work that could never be produced without a generous subsidy.

A. A. PEARSON

Manual of Bacterial Plant Pathogens, 2nd edition. By Charlotte Elliott. [*Annales Crytogamici et Phytopathologici*, vol. 10]. (Waltham, Mass.: The Chronica Botanica Co.; London: Wm. Dawson and Sons, Ltd., 1951.) 186 pp. Price 45*s*.

The arrival in this country of the second and enlarged edition of Dr Charlotte Elliott's *Manual of Bacterial Plant Pathogens* will be welcomed by the all-too-few plant pathologists actively engaged in the study of plant diseases caused by bacteria.

There are many more such diseases than most plant pathologists realize, and it is to be hoped that students will pay more attention to this subject in future, especially as regards economic plants which have sustained serious losses in our Empire and Commonwealth overseas. In fact, the shortage of trained bacteriologists is so acute that quite recently a disease of sugar cane in British Guiana could be investigated only by transferring, for a limited period, a pathologist from Nyasaland who had gained experience of the crop in Mauritius.

Since the publication of the first edition of the *Manual* in 1930, much new knowledge of the activities and relations of bacterial plant pathogens has accumulated, and Dr Elliott has herself contributed a considerable amount in this respect.

The book is dedicated to that small band of enthusiasts who worked under the late Dr Erwin F. Smith of the United States Department of Agriculture. As in the first edition the pathogens are given in alphabetical order, but the more recent classification and nomenclature of Bergey's *Determinative Bacteriology* has been adopted in place of that of Erwin Smith. Thus *Bacterium* becomes *Pseudomonas*, *Bacillus* becomes *Erwinia* and *Aplanobacter* is merged in *Corynebacterium*. The comparatively new genera *Xanthomonas* and *Agrobacterium* are also included; but whereas the former has been generally accepted, the latter has not.

The characters of every species are briefly described, synonyms are given and an admirable, though short, description of the main symptoms of disease follows which is perhaps one of the most valuable parts of the book. Host plants, geographical range and control measures are given for every pathogen, as also are references to the majority of papers published up to and including 1948.

The book is divided into two parts. The first deals with species of *Agrobacterium*, *Bacterium* (used as a temporary generic name), *Corynebacterium*, *Erwinia* (= *Bacterium* of Topley and Wilson and other authorities), *Pseudomonas* and *Xanthomonas* in that order and occupies pp. 3–154. The second part, pp. 155–167, headed 'Bacterial species in the literature from plants but not recognized as valid plant pathogens', while of interest to some is of little value for the main object of the book which is the identification of pathogens; it might well have been omitted as it is not complete and the only spore-former, *Bacillus polymyxa*, of which there is very good evidence of pathogenicity in Canada and Europe, is not included.

The book ends with two most useful and complete indexes, one of genera and species of host plants, the other of genera and species of bacteria.

It may be permissible to take the opportunity of drawing attention to the comparative failure in determinative bacteriology as regards adequate records of the biochemical activities of the bacteria concerned. Genera are not difficult to recognize, but it is a very different matter when one comes to distinguish species unless all the characters have been determined under stated conditions and are known in detail, which is not always the case. The species of *Pseudomonas*, for instance, closely resemble one another in their morphology, staining reactions and physiological characters. The most that can be done at present is to group them according to their behaviour towards gelatin and the sugars, always provided one knows in what medium the sugars are incorporated, whether peptone or peptone-free, the pH, temperature and duration (5 days or 3 weeks) of the observations.

The bald statement 'no acid in lactose' is meaningless by itself and needs considerable amplification. It has been shown that slight but definite *changes* in pH are constant and are quantitative reactions capable of measurement and repetition. The genus *Xanthomonas* presents a similar problem and the only sure means of establishing the identity of a given isolation is by inoculation under known conditions and reproduction of identical symptoms of disease.

It is to be regretted that the long delay in publishing this outstanding book has resulted in the absence of references to many important papers which have appeared during and since 1948.

The price of the manual is rather more than most students are prepared to pay and might have been somewhat reduced by curtailing the second part to a single page and omitting the five illustrations taken from Erwin Smith's works. The reproduction of the first page of Prof. Burrill's earliest report on fire blight of pear in 1877, while of interest to the history of the investigation of this disease, is however a little unfortunate as no mention is made therein of *bacteria*, the organisms which Burrill was the first to show were the cause of a plant disease. These additions are not essential for the main object in hand; but one can sympathize with the motives for their inclusion as they form a fitting and lasting memorial to that great investigator Erwin F. Smith.

Dr Elliott's manual should find a place in every biological library and is indispensable for all whose work lies in the domain of the bacterial diseases of plants.

W. J. DOWSON

The Intelligent Use of the Microscope, 2nd edition. By C. W. OLLIVER. (London: Chapman and Hall. 1951.) xii+192 pp., 59 text-figures. Price 15*s*.

Members will welcome the publication of the second edition of this sensible guide, by a fellow mycologist, to the art of handling the microscope. The companion art of preparing objects for examination is not dealt with. After a simplified illustrated introduction on optical principles, numerical aperture and resolution, a discussion follows on the choice of equipment suitable for various jobs. The sections on illumination, adjustment and testing will probably be the most valuable part of the book to the many already accustomed to use a compound microscope who are aware that the instrument can give much more if skilfully handled. This work shows the inexpert how to get an image or photograph as good as required without unnecessary fuss. The final chapter on phase contrast is a useful conclusion to this edition.

P.H.G.

Flora of the British Isles. By A. R. CLAPHAM, T. G. TUTIN and E. F. WARBURG. (Cambridge University Press. 1952). li+1591 pp. Price 50*s*.

Although there are plenty of modern books about British wild flowers and comparatively modern versions of some of the old and favoured floras, this is in fact the first new book giving standard descriptions of the British flora as a whole since Hooker's *Student's Flora of the British Islands* appeared in 1870, and everyone will surely agree that it was badly needed. Its real value can naturally not be assessed accurately until it has been given a thorough testing, but even a more or less casual glance through the pages reveals that it is a flora with a difference.

With few exceptions the descriptions of the 2500 species and subspecies listed have been drawn up afresh from living material or herbarium specimens and, wherever possible, the keys are based on characters that can be detected as well in the field as in the laboratory. Indeed, the book clearly reflects the great advances made by professional botanists during the present century in studying the ecology of plants and in a field approach to taxonomic problems. Side by side with the morphological descriptions is to be found information about the geographical and ecological distribution of the species and subspecies, their flowering period, method of pollination, seed-dispersal mechanism, number of chromosomes and life form.

Many introduced plants, either naturalized or of common occurrence, are included. Small initial letters have been adopted for all specific epithets, but apparently with some reluctance, for wherever appropriate the same name but with an initial capital for the epithet, has been rather wastefully repeated as a synonym. Those who are no longer students (as usually understood), and who have been content to cling to the past in nomenclature, will undoubtedly find the multitude of new names bewildering, and may feel inclined to join the ranks of those who fain would see the principle of *nomina conservanda* applied to specific epithets.

The authors state that the book is intended primarily for students and amateur botanists, and for professional botanists 'who are not taxonomic specialists but need to identify species without going into great detail in the so-called critical genera'. It should, however, be of the greatest value to anyone interested in field botany, even if they are specialists in certain groups, and not least to mycologists. The three authors, all keenly interested in ecology and 'field' taxonomy, and inspired by Sir Arthur Tansley, have indeed provided the mycologist with a modern field-book for identifying his host plants, and it is to be hoped that some of our younger mycologists, realizing the need for a similar systematic study of *fungi* in the field, will follow their lead and set about producing a companion volume of British fungi occurring on the wild plants described in this book.

W. C. MOORE

The Fungi of Hertfordshire. By P. H. GREGORY. *Transactions of the Hertfordshire Natural History Society and Field Club*, 23, pp. 135–208, 1951. 10*s.*

An annotated list such as this is useful and interesting to all of us. Hertfordshire now ranks high among those counties mycologically better known. Records accumulated during more than a century have been compiled in modern nomenclature and many new ones added. The earlier collectors sought and painted the larger fungi, especially the agarics; later the Myxomycetes and lichens were studied intensively by experts on these groups; then the late Alex. Smith and other professionals hunted the rusts and other pathogens. A good historical survey is given of the collectors of fungi in the county since about 1840.

We can now ascertain at a glance the fungi recorded from Hertfordshire. Specialists who can say 'such and such names of fungi should be removed from the list' should write to the Recorder of Fungi of the Hertfordshire Natural History Society; those who note lacunae will no doubt take the first opportunity to add new records.

G.R.B.

Review of Medical and Veterinary Mycology. (Commonwealth Mycological Institute, Kew, Surrey.) 10*s.* per annum post free.

During the past thirty years mycological plant pathologists in all parts of the world have relied on the *Review of Applied Mycology* to keep themselves up-to-date and to provide the keys to problems outside their own specialities. The hope of the late Sir Edwin Butler, first director of the Commonwealth Mycological Institute, that medical and veterinary mycologists might eventually be offered a similar service is now fulfilled by the appearance of the two latest issues of the *Annotated Bibliography of Medical Mycology* as Parts 9 and 10 of the *Review of Medical and Veterinary Mycology.* Hitherto issued annually, the new periodical will in future appear twice yearly and every student of mycoses of man and animals will probably consider a personal subscription to this unique journal, in which more than two thousand papers have already been abstracted, to be essential.

G. C. AINSWORTH

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Contributors are asked to be clear and concise, and to use a recent issue of the *Transactions* as a guide to the arrangement of headings and subheadings, explanations of plates and figures, references to the literature, and other details. Each paper should start with a short summary.

The standards adopted in the *Transactions* are those outlined in the Royal Society's pamphlet, *General Notes on the Preparation of Scientific Papers* (1950, Cambridge University Press, 200 Euston Road, London N.W. 1, price 2*s.* 6*d.*). An exception is that in the *Transactions* citations of references to literature, although based on the Harvard system, include the full titles of the papers and complete page numbers. Titles of journals are abbreviated in accordance with *A World List of Scientific Periodicals*, 1952.

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The attention of authors proposing new taxonomic groups is drawn to the need to give an adequate description and figure, and to designate the types as required by the *International Rules of Botanical Nomenclature.* The description of a new species should be accompanied by a figure, and whenever possible the type specimen should be deposited in one of the national herbaria.

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